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The trilobite Family Illaenidae Hawle et Corda, 1847 from the Ordovician of the Prague Basin (Czech Republic)

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ABSTRACT: This present revision of Bohemian Ordovician illaenid trilobites of the Prague Basin (Czech Republic) follows the recent evaluation of their systematic position. This revision contains redescriptions and illustrations of the type species of several illaenid genera, the most up-to-date references for those genera, and an assessment of their variability and also of the palaeobiogeographic distribution of some illaenid genera. Bohemian illaenids in several cases include the type species of globally distributed taxa, whose distinction has often been uncertain and controversial. The validity of the genera *Zbirovia* Šnajdr, 1956 and *Zdicella* Šnajdr, 1956 is discussed and confirmed. The genus *Alceste* Hawle et Corda, 1847 stays in open nomenclature. In *Ectillaenus katzeri katzeri* (Barrande, 1856) allometric growth is described and *Vysocania* Vaněk & Vokáč, 1997 is considered to be a junior synonym of *Stenopareia* Holm, 1886.

KEY WORDS: Bohemia, revision, systematic, Trilobita

The Family Illaenidae Hawle et Corda, 1847 is one of the most diverse Ordovician trilobite groups in the Prague Basin, being represented by 18 species assigned to nine genera. Illaenids first appear in the Arenig, in the upper part of the Klabava Formation where Mergl (1991, 1992) found indeterminable remains of *Ectillaenus* sp. in the *Nocturnellia* Community. The family reached a maximum diversity in the basin during the middle and late Ordovician and their last representative is *Stenopareia pulchella* Šnajdr, 1978 from the Llandovery Želkovice Formation (Šnajdr 1978).

1. Historical review

The Family Illaenidae has been known from the Ordovician of the Prague Basin since the first half of the nineteenth century. These trilobites were first studied by Barrande (1846a, b, 1852, 1856, 1872), who described 11 new species under the uniform generic designation *Illaenus* Dalman, 1827. At about the same time Hawle & Corda (1847) also examined these trilobites but the majority of their species were considered invalid by Barrande (1852, 1872). Illaenid trilobites were also studied in the Czech Republic at the beginning of twentieth century by Holub (1908), Klouček (1913, 1916), and Perner (1918) amongst others.

In 1954 Jaanusson re-revalued the morphology and systematic position of illaenid trilobites and described several new genera. The most recent detailed revisions of Czech illaenid trilobites were those of Šnajdr (1956, 1957, 1958, 1983a, b, 1984, 1986). Although Pek & Vaněk (1989) in their *Index of Bohemian Trilobites* presented substantial changes in the systematics of the illaenids, these were not accompanied by explanations, descriptions or illustrations.

Illaenid trilobites are geographically widespread and the type species of several genera came from the Prague Basin. These are amongst the taxa redescribed and illustrated in the present work.

2. Discussion of illaenid–cheirurid assemblages

Hammann (1992) noted that illaenid trilobites had a preference for intrashelf or shelf-edge carbonate buildups of various kinds; likewise they were prevalent in basin environments and siliciclastic sediments because they required a relatively rigid substrate. Illaenid trilobites are commonly associated with cheirurid trilobites (see Hammann 1992 and references therein), forming the illaenid–cheirurid community of Fortey (1975). Cocks & Fortey (1988) also pointed out that they formed part of the dalmanitid–calymenacean assemblage occurring in shallow-water clastic sediments, including those of Bohemia.

Illaenid trilobites are diverse and common (Fig. 1) in the Prague Basin, occurring both in typically shallow-water facies and in deeper-water sediments (e.g. in the black shales of the Šárka, Dobrotivá and Králův Dvůr formations) where the substrate would not be expected to be firm.

As noted by Slavíčková (1999a), the illaenids occur with dalmanitid and sometimes also with cyclopygid trilobites. Therefore the designation dalmanitid–illaenid–calymenacean assemblage is preferred for their occurrence in the Prague Basin.

Illaenid trilobites have limited stratigraphical importance in the Prague Basin, although some species are limited to one formation e.g. *Ectillaenus katzeri katzeri* (Salter, 1867), *E. benignensis* (Novák in Perner, 1918), *Zetillaenus wahlenbergianus* (Barrande, 1852) etc.

3. Palaeoautecology of illaenid trilobites

The palaeoautecology of illaenid trilobites has been discussed by several authors. Siegfried (1939) argued that representatives of the genus *lllaenus* Dalman, 1827 actively moved and swam on the sea bottom. Bergström (1973) argued that the life orientation of various illaenids was with the posterior end of the trilobite body hidden in the narrow burrow (see also Westrop 1983). Přibyl & Vaněk (1976) however, considered illaenids to

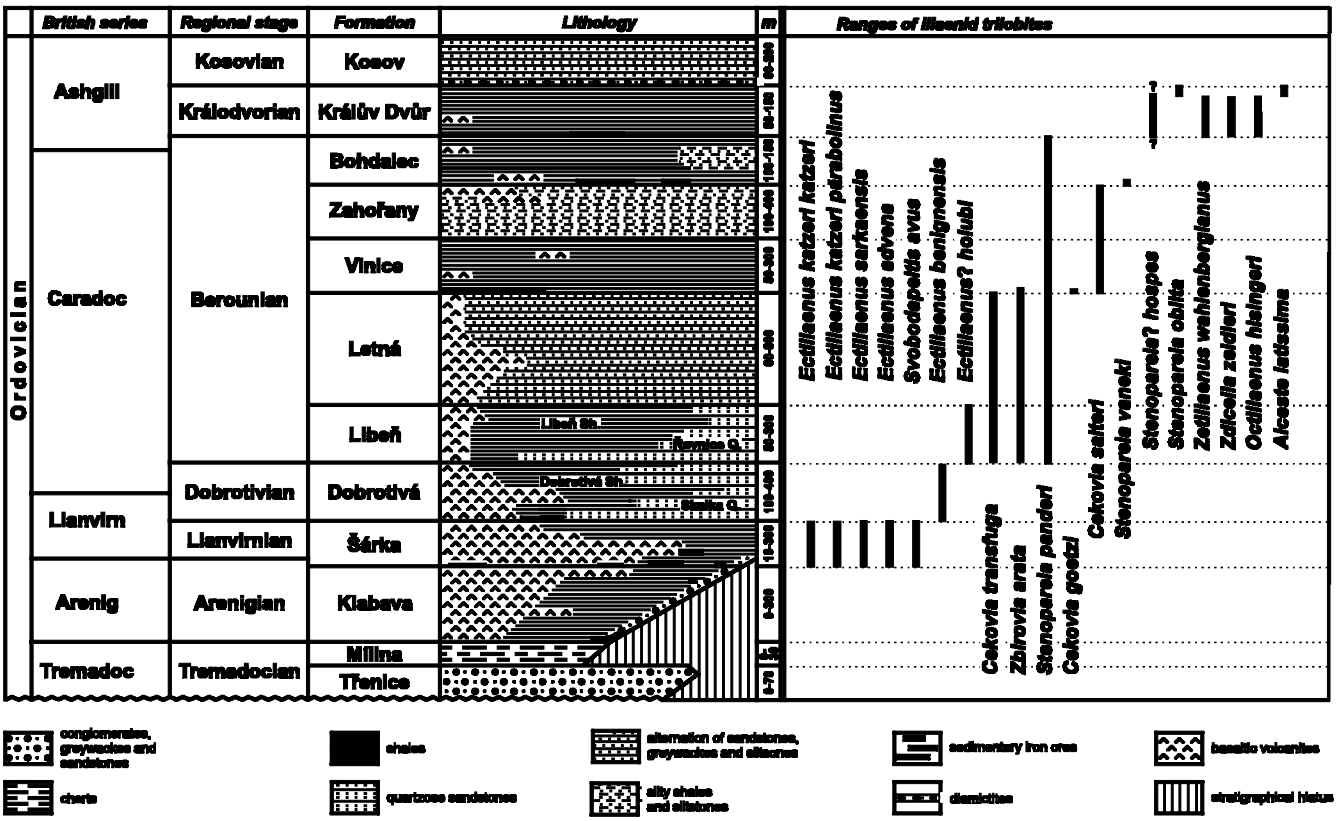

Figure 1 Distribution of illaenid trilobites in the Bohemian Ordovician (Havlíček 1992, modified). The correlation of British series and regional stages in the Lower and Middle Ordovician modified after Kraft *et al.* (2001).

have been good swimmers living near the sea bottom in deeper parts of the cold Ordovician sea, and searching for food by scraping the upper layers of the substrate.

Schmalfuss (1978) concluded that illaenids were filter feeders, resting on the substrate or in a shallow scraping thereon, with the posterior and anterior ends of the exoskeleton elevated, giving the concave curvature seen in some specimens. He suggested that they generated a flow of water by the action of exites and filtered it. Whittington (1997) considered that many illaenids may have been vagrant benthos, particularly well adapted for negotiating irregular surfaces, a view endorsed by Slavíčková (1999b), who also argued that the occurrence of concavely bent exoskeletons from the Ordovician of the Prague Basin reflected exuviation rather than the original life attitude.

4. Geological setting

The only non-metamorphosed, weakly tectonised and almost complete Lower Palaeozoic sequence in the Bohemian Massif is preserved in the so-called Barrandian area (Štorch *et al.* 1999). This area is composed of sedimentary and volcanic complexes of three superimposed basins, each of them representing a distinct tectonostratigraphical megacycle: Precambrian, Cambrian and Ordovician–Middle Devonian. The last of these began in the Tremadoc when a major marine transgression occurred in the newly formed Prague Basin with its longitudinal axis along a subsiding SW–NE tectonic zone striking at about 20° to the former, Cambrian, Příbram-Jince Basin (Štorch *et al.* 1999). Sedimentation persisted up to the Middle Devonian without any prominent breaks. The Ordovician strata are typically siliciclastic deposits which were replaced by limestone facies from the middle of the Silurian. Devonian limestone sedimentation was terminated by siliciclastic flysch deposits during the Givetian.

5. Remarks on distribution

Illaenid trilobites occur in a wide range of lithofacies in the Prague Basin (Fig. 1). Fine-grained, hard siliceous concretions of the Šárka and Dobrotivá formations contain undeformed, and three-dimensionally preserved fossils. Illaenid trilobites are similarly preserved in the pelocarbonate concretions and intercalations of the Zahořany and Králův Dvůr formations. Illaenids occurring in the black clay shales of the Šárka, Dobrotivá, Vinice, Zahořany, Bohdalec and Králův Dvůr formations have deformed exoskeletons with indistinct morphological details. Poorly preserved fossils, mostly internal moulds, come from quartzite sandstones of the Libeň, Letná and Zahořany formations. Illaenid trilobites are well preserved, with fine morphological details, in the unusual oolitic iron ores of the Vinice and Bohdalec formations. The stratigraphical distribution of illaenid trilobites from the Ordovician of the Prague Basin is given in Figure 1 and detailed information on their occurrence was recorded by Slavíčková (1999a).

6. Systematic palaeontology

Figured and cited specimens are housed in the following institutions: National Museum of Prague (NM), Czech Geological Survey (CGU), Faculty of Natural Science of the Charles University (CHU), Museum of B. Horák in Rokycany (MR).

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Class Trilobita Walch, 1771
Order Corynexochida Kobayashi, 1935
Suborder Illaenina Jaanusson, 1959
Family Illaenidae Hawle et Corda, 1847

Remarks. In this work the division of the Suborder Illaenina into the Families Illaenidae and Styginidae has been accepted and subfamilies within the Illaenidae have not been recognised (see Lane & Thomas 1983). There has been considerable discussion on the classification of illaenid trilobites over the last 50 years and most recently Whittington (1997) has addressed some of the issues and produced a diagnosis of the family.

Genus *Ectillaenus* Salter, 1867

Type species. *Illaenus Perovalis* Murchison, 1839 from the Llanvirn of Shropshire, England.

Remarks. The genus *Ectillaenus* was defined by Salter (1867) originally as a subgenus of *Illaenus* Dalman, 1827. Its validity was not accepted for a considerable time (e.g. Holub 1908; Raymond 1916; Perner 1918). Raymond (1916) established the genus *Wossekia* with the type species *Illaenus katzeri* Barrande, 1856 from the Ordovician of the Prague Basin. Warburg (1925) doubted the validity of Raymond's genus and Whittard (1940, 1956) considered *Wossekia* to be a junior synonym of *Ectillaenus*. Přibyl (1953) retained *Ectillaenus* as a subgenus of *Illaenus* but other authors over the past 60 years have given it generic status (e.g. Jaanusson 1954, 1959; Šnajdr 1957; Fortey & Owens 1987; Rábano 1989; Pek & Vaněk 1989; Pillet 1990; Hammann 1992).

Ectillaenus differs from other illaenids in having shorter axial furrows, parabolic or oval outlines of cephalon and pygidium, and 10 thoracic segments. The genus is distributed in Gondwana and its marginal terranes. It occurs in the Czech Republic (Perner 1918; Šnajdr 1957), Sweden (Kielan 1960), Bulgaria (see Rábano 1989), England (Whittard 1956; Kennedy 1989), Wales (Fortey & Owens 1987), France (Pillet 1990), Portugal (see Pillet 1990), Spain (Rábano 1989; Pillet 1990) and in an Asian Republic of the former Soviet Union (see Rábano 1989) in rocks of Arenig to Ashgill (Jaanusson 1959).

Bohemian taxa comprise: *Ectillaenus katzeri katzeri* (Barrande, 1856); *E. katzeri parabolinus* (Novák *in* Perner, 1918); *E. advena* (Barrande, 1872); *E. benignensis* (Novák *in* Perner, 1918); *E.*? *holubi* (Šnajdr, 1956); *E. sarkaensis* (Novák *in* Perner, 1918).

Ectillaenus katzeri katzeri (Barrande, 1856)
(Figs 2a–e, 3a–f, 4c–d, f)

1856 *Illaenus katzeri* Barrande; Barrande, p. 2.
1872 *Illaenus katzeri* Barrande; Barrande, p. 72, pl. 5, figs 28–37, pl. 6, figs 1–4, pl. 14, fig. 36.
1916 *Wossekia katzeri* (Barrande); Raymond, p. 14.
1918 *Illaenus katzeri* Barrande; Perner, pp. 21, 22, pl. 3, figs 19–22.
1918 *Illaenus parabolinus* Novák; Perner, pl. 2, figs 7–9.
1925 *Illaenus katzeri* Barrande; Warburg, pp. 99, 100.
1940 *Ectillaenus katzeri* (Barrande); Whittard, p. 142.
1954 *Ectillaenus katzeri* (Barrande); Jaanusson, pp. 549, 550, 576; text figs 3, 18.
1957 *Ectillaenus katzeri* (Barrande); Šnajdr, pp. 212–17, pl. 2, figs 9–15; pl. 4, fig. 9; pl. 6, fig. 3; pl. 10, fig. 12.
1957 *Ectillaenus parabolinus* (Novák); Šnajdr, pl. 4, fig. 8; pl. 6, fig. 8.
1970 *Ectillaenus katzeri* (Barrande); Horný & Bastl, pp. 180–82.
1989 *Ectillaenus katzeri* (Barrande); Pek & Vaněk, p. 17.
1990 *Ectillaenus katzeri* (Barrande); Pillet, p. 20.

Lectotype. Complete specimen NM L 19722 from the Šárka Formation at Osek near Rokycany. Figured by Barrande (1872, pl. 5, figs 28, 29). Lectotype designated by Šnajdr (1957).

Other material. Several tens of almost complete specimens, hundreds of cephalic and pygidial shields.

Diagnosis. *Ectillaenus* species with minute eyes composed of several tens of lenses situated in the first third of the cephalon, in palpebral view. Librigenae narrow (tr.) and extended in small inwardly rounded genal angles. Thoracic axis is widest at the fourth or fifth segment. Pygidial axis indistinct, short, reaching maximally one-third of the pygidial length in dorsal view. Anterior borders of pygidium bent moderately inwards.

Description. Cranidium strongly vaulted, mostly semicircular (young holaspids) or parabolic in dorsal outline (older holaspids). Axial furrows occupy approximately first third of the cephalic length (in palpebral view), being slightly outwardly curved in the middle part of their course. Five pairs of muscle scars are present. Occipital, anterior, lateral and middle pairs oval in outline except the largest kidney-shaped basal muscle pair. On the glabella of young specimens an axial keel-like elevation is present.

Librigenae laterally extended with rounded genal angles. Minute eyes, composed of several tens of lenses, are located opposite the middle part of the axial furrows.

Rostral plate transversally extended, crescentic. Surface sculpture consisting of about 10 long, unbranched terrace lines parallel to the rostral suture.

Anterior margin of hypostome slightly arched. Hypostomal wings transversally extended and narrowing outwards. Hypostomal lobe vaulted, subtrapezoidal in outline with terrace lines.

Thorax consisting of ten segments. Axis tapering posteriorly, the maximum width is at the fourth or fifth segment.

Pygidium vaulted, parabolic in outline. Pygidial axis weakly defined (except for young holaspids), tapering backwards, at first markedly then more gently. Length of pygidial axis variable: in several cases dark axial rings are present (NM L 33192 possesses three axial rings, NM L 32596 two pygidial pleurae and four axial rings, MR 9832 and MR 149 two rings, CGU PP 102 three rings). Pygidial doublure wide, especially in the post-axial part of the pygidium where a longitudinal groove is evident. Doublure bears long terrace lines parallel with the posterior margin of the pygidium.

Exoskeleton covered with fine, dense pits, together with terrace lines. Where the glabellar muscle scars are present, the sculpture is interrupted or weakly developed and chaotically arranged.

Ontogeny. In this subspecies a high degree of intraspecific variability exists and allometric growth is evident. The cephalon of young holaspids is semicircular and the pygidium is oval in outline with very distinct and long axial furrows. With increasing size, the cephalon and pygidium become more parabolic in outline with shorter and less easily perceptible axial furrows. Similar allometric growth was described by Hammann (1992) in the illaenid species *Cekovia perplexa perplexa* Hammann, 1992 and by Hughes & Chapman (1995) in the Silurian aulacopleurine *Aulacopleura konincki* (Barrande, 1846).

Remarks. Specimens illustrated by Perner (1918) and Šnajdr (1957) as *E. parabolinus* (Novák in Perner, 1918) represent older holaspid exoskeletons of *E. katzeri katzeri* in which the outline of the cephalon is parabolic. *E. katzeri katzeri* is the most widely distributed *Ectillaenus* species in the Šárka Formation and differs from other Bohemian Llanvirn illaenids in having minute eyes situated in the first third of the cephalon (in palpebral view), and parabolic outlines of the cephalon and pygidium. *E. katzeri parabolinus* (Novák in Perner,

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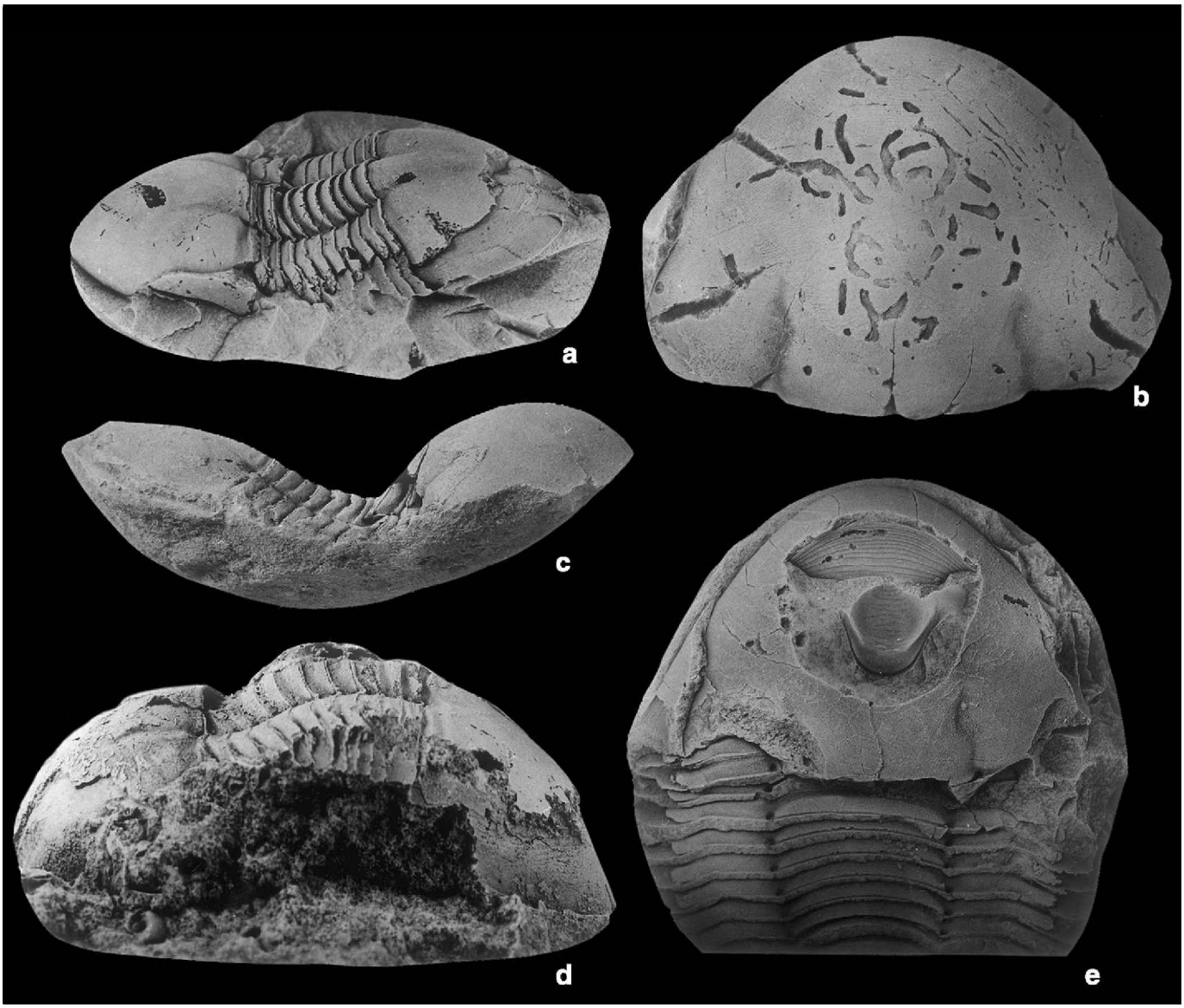

Figure 2 *Ectillaenus katzeri katzeri* (Barrande, 1852): (a) oblique lateral view on concavely flexed specimen NM L 33037, ×1·5, Šárka Formation, Praha-Šárka; (b) cranidium NM L 32627, ×1·4, Šárka Formation, Osek; (c) lateral view of concavely flexed specimen NM L 32636, ×1·3, Šárka Formation, Osek; (d) lateral view of convexly flexed specimen NM L 32457, ×2, Šárka Formation, Osek; (e) incomplete specimen with hypostome and rostrum *in situ* NM L 16737, ×1·5, Šárka Formation, Osek.

1918), *E. sarkaensis* (Novák in Perner, 1918) and *E. advena* (Barrande, 1872) also occur with *E. katzeri* in the Bohemian Šárka Formation. The first two are mostly restricted to the eastern part of the basin, and the latter occurs in both the eastern and western parts. Unfortunately the Šárka Formation is undivided and the precise stratigraphical levels of the siliceous concretions in which almost all the known specimens occur remain unknown. It cannot therefore be proved if they occur at different stratigraphical levels.

From the type species, *E. perovalis* (for description see e.g. Whittard 1961, Fotey & Owens 1987; Kennedy 1989) is distinguished in having minute eyes, a more parabolic outline of the cephalon and pygidium and more gentle sculpture. *E. giganteus* (Burmeister, 1843) possesses larger eyes and a wider pygidium (tr.) semicircular in outline.

Occurrence. Šárka Formation, Czech Republic.

Ectillaenus katzeri parabolinus (Novák in Perner, 1918)
(Fig. 4a–b)

1918 *Illaenus parabolinus* Novák; Perner, pp. 20, 21, 26; pl. 2, figs 1– 6.
non 1918 *Ectillaenus parabolinus* (Novák); Perner, pl. 2, figs 7–9. (= *Ectillaenus katzeri katzeri*)
1954 *Ectillaenus parabolinus* (Novák); Jaanusson, p. 577.
1957 *Ectillaenus parabolinus (*Novák); Šnajdr, pp. 207–12, pl. 6, figs 4–7.
non 1957 *Ectillaenus parabolinus* (Novák); Šnajdr, pl. 4, fig. 8; pl. 6, fig. 8. (= *Ectillaenus katzeri katzeri*)
1961 *Ectillaenus parabolinus (*Novák and Perner); Whittard, p. 215.
1970 *Ectillaenus parabolinus* (Novák *in* Perner); Horný & Bastl, p. 233.

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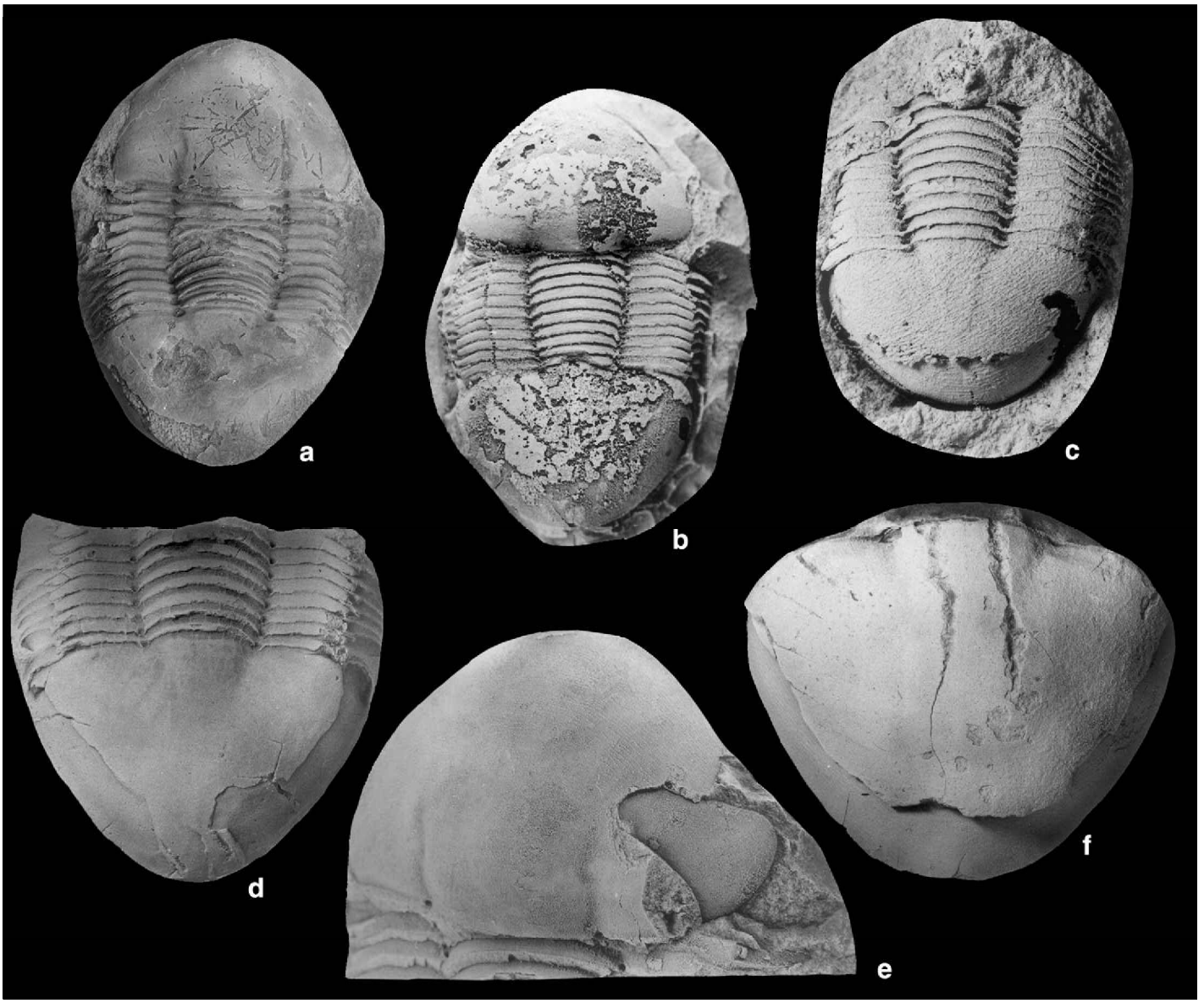

Figure 3 *Ectillaenus katzeri katzeri* (Barrande, 1852): (a) almost complete specimen NM L 16722, lectotype, ×0·9, Šárka Formation, Osek; (b) almost complete specimen CHU 655, ×1·2, Šárka Formation, Praha-Vokovice; (c) pygidium of young holaspid specimen with oval outline NM L 32524, ×8, Šárka Formation, Osek; (d) pygidium of older holaspid specimen with parabolic outline NM L 32516, 1·6, Šárka Formation, Osek; (e) cephalon with displaced librigena with rostrum *in situ* NM L 19243, ×1·8, Šárka Formation, Mýto; (f) pygidium of large holaspid specimen NM L 32577, ×1·1, Šárka Formation, Osek.

1989 *Ectillaenus parabolinus* (Novák *in* Perner); Pek & Vaněk, p. 17.

Lectotype. Cephalon with a part of thorax NM L19236 from the Šárka Formation at Praha-Šárka. Figured by Perner (1918, pl. 2, figs 3–6). Lectotype designated by Šnajdr (1957).

Other material. Several cephala, two incomplete specimens.

Diagnosis. Subspecies of *Ectillaenus katzeri* with parabolic anterior margin of cephalon. Cephalon strongly vaulted in its posterior part, anteriorly vaulting disappears.

Remarks. In the course of the revision it was found that the majority of cephala considered by earlier workers as *E. parabolinus* are actually mature holaspids of *E. katzeri* but with a more parabolic anterior part of cephalon. *E. katzeri katzeri* possesses a less parabolic cephalon vaulted in its whole profile. *E. parabolinus* is considered as a subspecies of *E. katzeri* (Barrande, 1856), rare in the Šárka Formation and has been found only in the eastern part of the Prague Basin. It may represent a descendant of *E. katzeri katzeri*, but unfortunately as is noted above, the precise stratigraphical levels of siliceous concretions containing all the existing specimens are not known.

Occurrence. Šárka Formation, Czech Republic.

Ectillaenus sarkaensis (Novák in Perner, 1918)
(Figs 4e, g, 5a–f)

1918 *Illaenus šárkaënsis* Novák; Perner, pp. 21, 22, 27; pl. 2, figs 10–14.
1940 *Ectillaenus sarkaensis* (Novák and Perner); Whittard, p. 142.
1954 *Ectillaenus šarkaensis* (Novák); Jaanusson, p. 576.
1957 *Ectillaenus šarkaensis* (Novák); Šnajdr, pp. 217–23, pl. 3, figs 1–7; pl. 5, fig. 11.
1961 *Ectillaenus hughesi* (Hicks); Whittard, p. 215.
1970 *Ectillaenus sarkaensis* (Novák *in* Perner); Horný & Bastl, pp. 275, 276.

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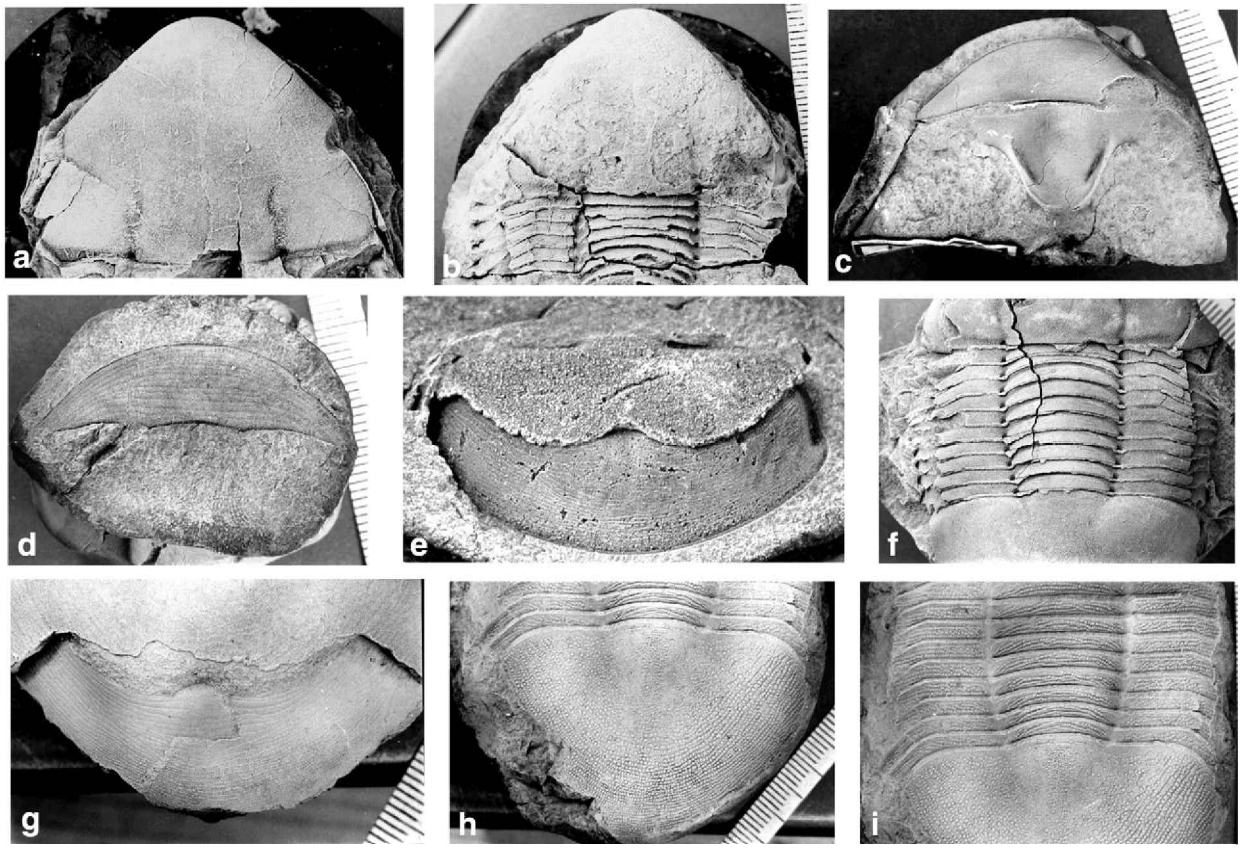

Figure 4 *Ectillaenus katzeri parabolinus* (Novák in Perner, 1819): (a) cranidium NM L 19208, ×1·2, Šárka Formation, Praha-Šárka; (b) almost complete cephalon with part of thorax, lectotype, NM L 19236, ×0·9, Šárka Formation, Praha-Šárka. *Ectillaenus katzeri katzeri* (Barrande, 1856); (c) rostrum and hypostome NM L 34581, ×1·1, Šárka Formation, Osek; (d) rostrum NM L 34580, ×1·3, Šárka Formation, Osek; (f) thorax NM L 32560, ×1·1, Šárka Formation, Osek. *Ectillaenus sarkaensis* (Novák in Perner, 1918); (e) doublure of pygidium with terrace lines NM L 35274, ×5·7, Šárka Formation, Praha-Šárka, Vokovice (cihelna). *Ectillaenus benignensis* (Novák in Perner, 1918); (g) doublure of pygidium with terrace lines NM L 32679, ×1·1, Dobrotivá Formation, Praha-Bubeneč; (h) sculpture of pygidium, negative NM L 32679, ×0·9, Dobrotivá Formation, Praha-Bubeneč; (i) sculpture of thorax, negative NM L 32679, ×0·9, Dobrotivá Formation, Praha-Bubeneč.

1982 *Ectillaenus sarkaensis* (Novák); Gil Cid & Rábano, pp. 1, 2, figs 1, 5.
1989 *Ectillaenus sarkaensis* (Novák *in* Perner); Pek & Vaněk, p. 17.
1990 *Ectillaenus sarkaensis* (Novák); Pillet, p. 20.

Lectotype. Incomplete specimen NM L19238 from the Šárka Formation at Praha-Šárka. Figured by Perner (1918, pl. 2, figs 10–14). Lectotype designated by Šnajdr (1957).

Other material. Several tens of complete specimens, cephala and pygidia.

Diagnosis. Blind *Ectillaenus* species with wide cephalon. Fixigenae twice as wide as librigenae (tr.). Pygidium wider than long with semicircular posterior border, axis reaching one-third of its length in dorsal view.

Ontogeny. One transitory pygidium of a meraspid specimen with two unreleased segments was found (NM L 33066). It resembles the pygidial shield of holaspids in its wide oval outline.

Remarks. *E. sarkaensis* was validly described by Perner (1918) but prior to this date was mentioned by several authors as *nomen nudum*. The validity of this species was discussed by Whittard (1940, 1961), who considered that *E. sarkaensis* and *E. benignensis* (Novák *in* Perner, 1918) belonged in *E. hughesi* (Hicks, 1875). Following Šnajdr (1957) and Fortey & Owens (1987), I consider them as three separate species.

It is distinguished from *E. perovalis* by its wider cephalon and pygidium, oval in outline. Anterior borders of pygidium are not so sharply sloped and the sculpture is more subdued. The most similar Bohemian species is *E. benignensis*; it is also blind but with coarser sculpture and narrower outlines of cephalon and pygidium.

E. sarkaensis differs from other Bohemian species in having a markedly wider outline of cephalon and pygidium, and lack of eyes.

Occurrence. Šárka Formation, Czech Republic. Šnajdr (1957) mentioned that *E. sarkaensis* occurs only in the eastern part of the Prague Basin. In the course of the present study, three specimens of this species were found in material coming from near the town of Rokycany in the western part of the basin.

Ectillaenus advena (Barrande, 1872)
(Fig. 6a–e)

1872 *Illaenus advena* Barrande; Barrande, p. 66, pl. 6, figs 5–10; pl. 14, figs 37, 38.
1916 *Illaenus advena* Barrande; Raymond, p. 12.
1918 *Illaenus advena* Barrande; Perner, p. 26.
1957 *Ectillaenus advena (*Barrande); Šnajdr, pp. 203–207, pl. 2, fig. 8; pl. 6, fig. 2.
1970 *Ectillaenus advena* (Barrande); Horný & Bastl, p. 53.
1989 *Ectillaenus advena* (Barrande); Pek & Vaněk, p. 17.

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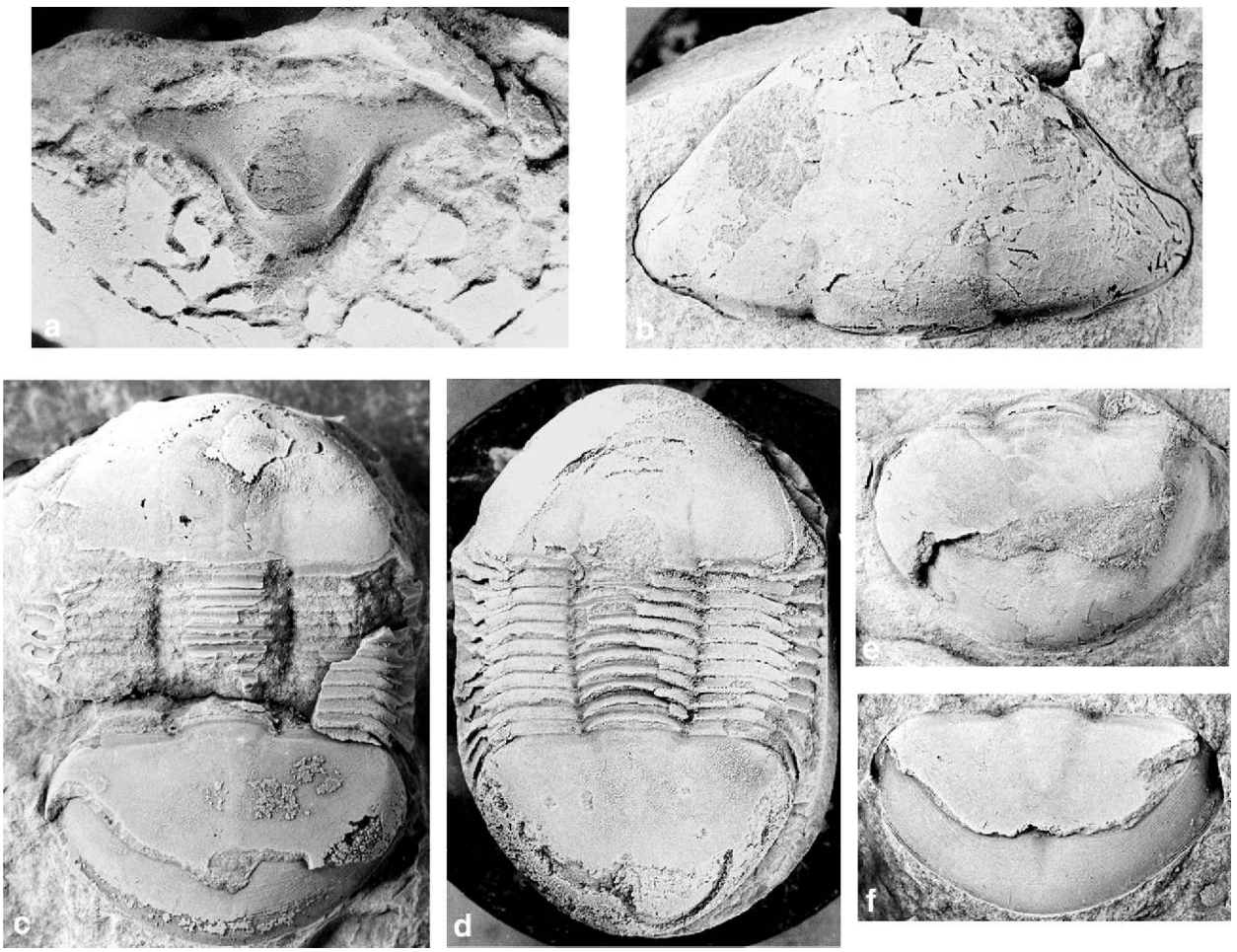

Figure 5 *Ectillaenus sarkaensis* (Novák in Perner, 1918): (a) cephalon with rostrum *in situ* NM L 19284, ×5, Šárka Formation, Praha-Vokovice; (b) cephalon NM L 33043, ×1·8 Šárka Formation, Praha-Šárka; (c) complete specimen, lectotype, NM L 19238, ×1·9, Šárka Formation, Praha-Šárka; (d) complete specimen NM L 23588, ×18·8, Šárka Formation, Praha-Šárka; (e) pygidium NM L 33043, ×1·2, Šárka Formation, Praha-Šárka; (f) pygidium NM L 32653, ×2, Šárka Formation, Praha-Vokovice.

Lectotype. Enrolled specimen with hypostome *in situ* NM L16740 from the Šárka Formation at Osek near Rokycany. Figured by Barrande (1872, pl. 6, fig. 5). Lectotype was designated by Šnajdr (1957).

Other material. Several incomplete specimens, tens of cephala and pygidia.

Diagnosis. *Ectillaenus* species with relatively large eyes composed of several hundred lenses situated in the first third of the cephalic length in palpebral view. Glabella wide in the posterior part, fixigenae narrow (tr.). Axis of thorax of the same width (tr.) as the first anterior thoracic segments and slightly tapering posteriorly. Pygidium with parabolic posterior border and distinct axis reaching over one-third of the pygidial length in dorsal view.

Remarks. In contrast to other Bohemian *Ectillaenus* species, *E. advena* has relatively larger eyes composed of several hundred lenses, a wide glabella and wide axis of the thorax. These features place it closer to some Scandinavian illaenids such as *Parillaenus* Jaanusson, 1954. It may be distinguished therefrom, however, by the different shape of the pygidium which is longer, triangular and with a distinctly parabolic posterior border. The most similar to *E. advena* is *E. katzeri katzeri*, but *E. advena* possesses larger eyes, a wider thoracic axis and a more rounded pygidium. It is distinguished from *E. giganteus* in having larger eyes and a more parabolic outline of the pygidium.

Occurrence. Šárka Formation, Czech Republic.

Ectillaenus benignensis (Novák *in* Perner, 1918)
(Figs 4g–i, 7a–e)

1918 *Illaenus benignensis* Novák; Perner, p. 26, pl. 2, figs 17–26.
1940 *Ectillaenus perovalis* form *hughesi* (Hicks); Whittard, p. 142.
1954 *Ectillaenus benignensis* (Novák), Jaanusson, p. 476.
1957 *Ectillaenus benignensis* (Novák), Šnajdr, pp. 196–203, pl. 1, figs 1–8; pl. 2, figs 1–7; pl. 4, figs 1–7.
1961 *Ectillaenus hughesi* (Hicks); Whittard, p. 215.
1970 *Ectillaenus benignensis* (Novák *in* Perner); Horný & Bastl, pp. 71, 181.
1984 *Ectillaenus benignensis* (Novák); Šnajdr, p. 21, figs 4–7.
1989 *Ectillaenus hughesi* (Hicks); Pek & Vaněk, p. 17.

Lectotype. Incomplete specimen NM L19232 from the Dobrotivá Formation at Sv. Dobrotivá. Figured by Perner (1918, pl. 2, figs 17–20). Lectotype designated by Šnajdr (1957).

Other material. Several tens of cephala, pygidia and a number of completely preserved exoskeletons.

Diagnosis. Blind representative of *Ectillaenus* with semicircular cephalon. Fixigenae more than double the width (tr.) of librigenae. Pygidium parabolic in outline with straight and short anterior borders; lateral borders are sharply sloping.

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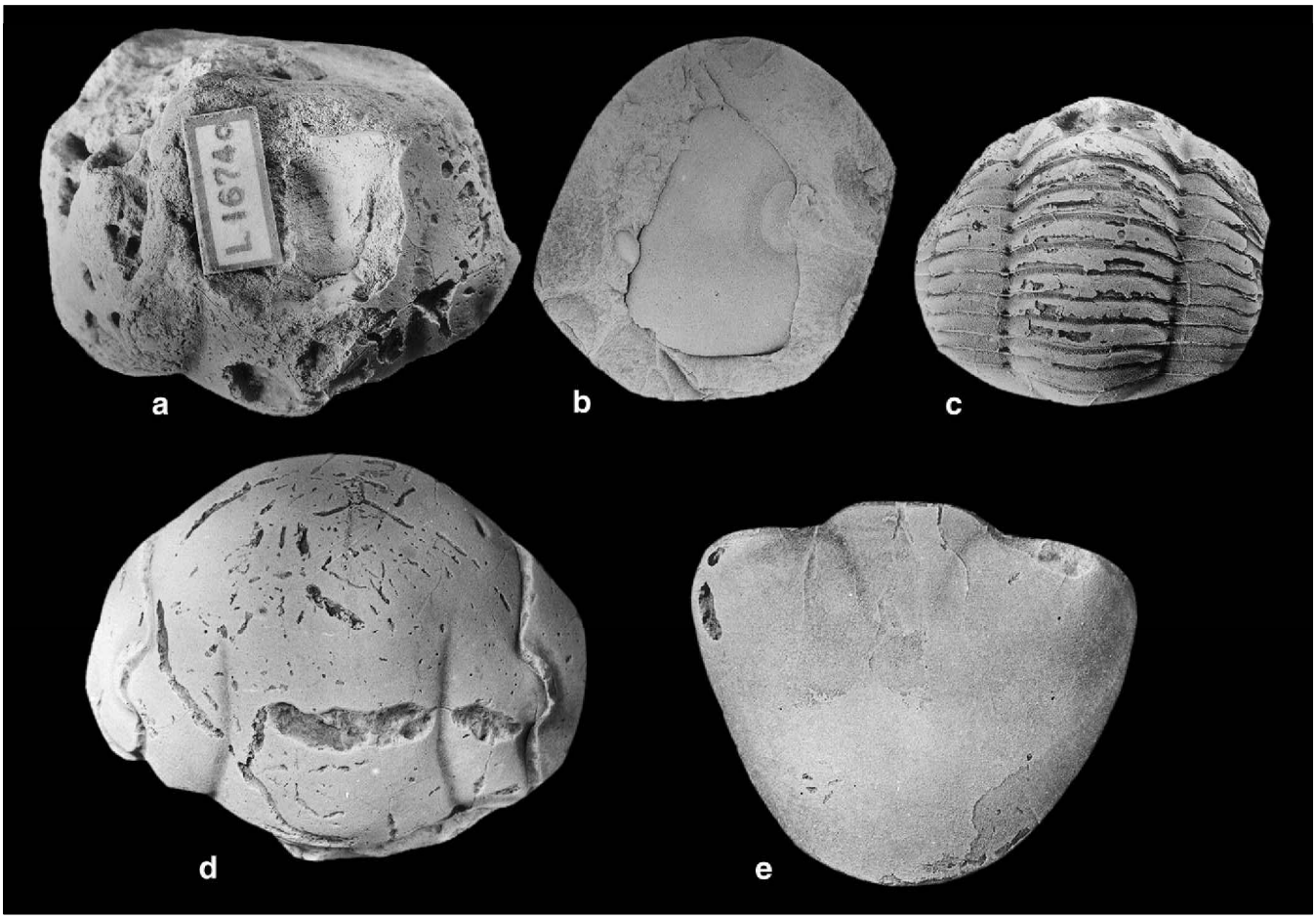

Figure 6 *Ectillaenus advena* (Barrande, 1872): (a) incomplete cephalon with hypostome *in situ*, lectotype, NM L 16740, ×1·6, Šárka Formation, Osek; (b) librigena with eye NM L 16743, ×0·9, Šárka Formation, Osek; (c) thorax NM L 16740, lectotype, 0·9, Šárka Formation, Osek; (d) cephalon NM L 16741, ×1·5, Šárka Formation, Osek; (e) pygidium NM L 33042, ×2, Šárka Formation, Osek.

Pygidial axis distinct, reaching maximally half of the pygidial length in dorsal view. Strong sculpture of large pits arranged mostly in rows.

Ontogeny. In the course of this revision, meraspid specimens with three (NM L 19229), four (NM L 19239, CGU MŠ 693) and five (CGU MŠ 694) unreleased segments on the transitory pygidia were found, and also a cephalon probably belonging to a meraspid or young holaspid specimen (NM L 33041); this cephalon is vaulted and parabolic in outline, with long axial furrows. Pygidium moderately parabolic in outline. Pygidial axis long, distinct, bearing axial rings.

Remarks. *E. benignensis* was first described by Perner (1918), and although Whittard (1940, 1961) considered *E. benignensis* to be a synonym of *E. hughesi* (Hicks, 1875), this was accepted only by Pek & Vaněk (1989). Šnajdr (1984) also discussed the question of the validity of *E. benignensis* but noted several differences between these two species: the shape of the fixigenae, cephalon and pygidium, the width of the pygidial doublure, the sculpture and also its stratigraphical occurrence. Fortey & Owens (1987) also considered the Czech species *E. benignensis* as valid. *E. benignensis* also possesses a more parabolic outline of the cephalic and pygidial shields.

E. benignensis differs from the other Bohemian representatives of the genus in having no eyes and a coarse sculpture. *E. sarkaensis* is also blind but *E. benignensis* differs from that species in its more parabolic and narrower outlines of cephalon and pygidium and in having obliquely sloping lateral borders of the pygidium.

It could represent a younger descendant of *E. sarkaensis*, probably living in a different environment.

Occurrence. Dobrotivá Formation, Czech Republic.

Ectillaenus? *holubi* (Šnajdr, 1956)
(Fig. 8c)

1956 '*Illaenus holubi*' n. sp.; Šnajdr, pp. 495, 496, pl. 1, fig. 1.
1957 *Ectillaenus holubi* (Šnajdr); Šnajdr, pp. 223, 224, pl. 1, fig. 9.
1970 *Ectillaenus holubi* (Šnajdr); Horný & Bastl, p. 168.
non 1988 *Ectillaenus*? *holubi* (Šnajdr); Moravec, p. 344, pl. 1, figs 1–5. (= *Stenopareia panderi*)
1989 *Ectillaenus holubi* (Šnajdr); Pek & Vaněk, p. 17.
1992 ?*Ulugtella holubi* (Šnajdr); Hammann, p. 76.

Holotype. Pygidium NM L19265 from the Libeň Formation at Čilina hill near Rokycany, Šnajdr (1956, pl. 1, fig. 9).

Other material. Two pygidia.

Diagnosis. A species with vaulted pygidium, especially in its anterior part referred with some doubt to *Ectillaenus*. Pygidium semicircular in outline, lateral borders obliquely sloping. Pygidial axis indistinct.

Remarks. Hammann (1992) suggested that this species might belong to the genus *Ulugtella* Petrunina, 1975. However, the lateral margins of the pygidium *E.*? *holubi* are not as angular as those of *Ulugtella;* it is here placed tentatively in *Ectillaenus* Salter, 1867. *E.*? *holubi* is distinguished by its heart-shaped

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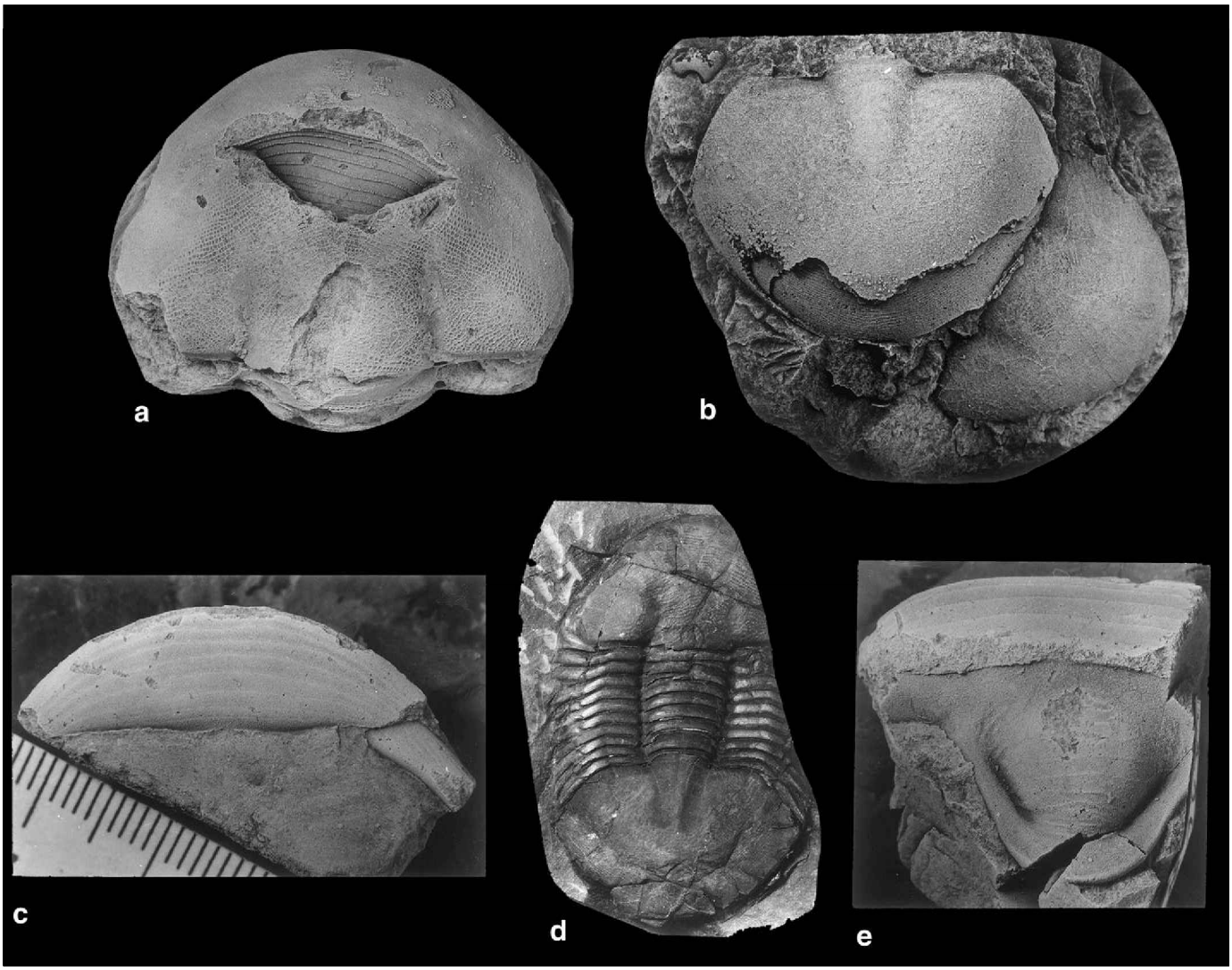

Figure 7 *Ectillaenus benignensis* (Novák in Perner, 1918): (a) cranidium NM L 33044, ×1·3, Dobrotivá Formation, Praha-Vokovice; (b) pygidium and cranidium NM L 32771, ×2, Dobrotivá Formation, Praha-Vokovice; (c) rostrum NM L 36012, ×2, Dobrotivá Formation, Praha-Vokovice; (d) almost complete specimen, lectotype, NM L 19232, ×0·7, Dobrotivá Formation, Sv. Dobrotivá; (e) hypostome NM L 32680, ×2, Dobrotivá Formation, Malé Přílepy.

pygidium with obliquely sloping lateral borders and semicircular posterior part of the pygidium. It differs from *Stenopareia panderi* in having a narrower outline, and sharply cut lateral borders, of the pygidium.

E.? holubi resembles *Zbirovia arata* (Barrande, 1872) but has moderately cut lateral margins of the pygidium and a posterior margin which is more circular in outline. For *Z. arata* the broad oval outline of the posterior margin is typical.

Occurrence. Rare species in the Libeň Formation, Czech Republic. Moravec (1988) described cephala and pygidia of *E.*? *holubi* from the Libeň and Vinice formations. Unfortunately, this material has been lost, but from the photographs (Moravec 1988) it is likely that it belonged in *Stenopareia panderi* (Barrande, 1852).

Genus *Octillaenus* Salter, 1867

Type species. *Illaenus hisingeri* Barrande, 1846 from the Králův Dvůr Formation, Králův Dvůr, Czech Republic.

Remarks. *Octillaenus* is characterised by having eight thoracic segments, a well-defined glabella and a long, first thoracic segment wider than the others.

Octillaenus occurs in the Ashgill of Sweden (Troedsson 1924) and Czech Republic (Salter 1867; Šnajdr 1957), where it is represented by *O. hisingeri* (Barrande, 1846).

Octillaenus hisingeri (Barrande, 1846)
(Fig. 8a–b, d)

1846b *Illaenus hisingeri* Barrande; Barrande, p. 14.
1852 *Illaenus hisingeri* Barrande; Barrande, p. 681, pl. 29, figs 25–29.
1867 *Illaenus (Octillaenus) hisingeri* (Barrande); Salter, p. 182, text fig. 46.
1916 *Octillaenus hisingeri* (Barrande); Raymond, p. 9, 14.
1924 *Illaenus hisingeri* Barrande; Troedsson, pp. 215–24, text figs 1–9.
1925 *Octillaenus hisingeri* (Barrande); Warburg, p. 98.
1954 *Octillaenus hisingeri* (Barrande); Jaanusson, pp. 568, 569, text fig. 14.
1957 *Octillaenus hisingeri* (Barrande); Šnajdr, pp. 155–9, pl. 7, figs 1–2.
1970 *Octillaenus hisingeri* (Barrande); Horný & Bastl, pp. 164, 165, 190.

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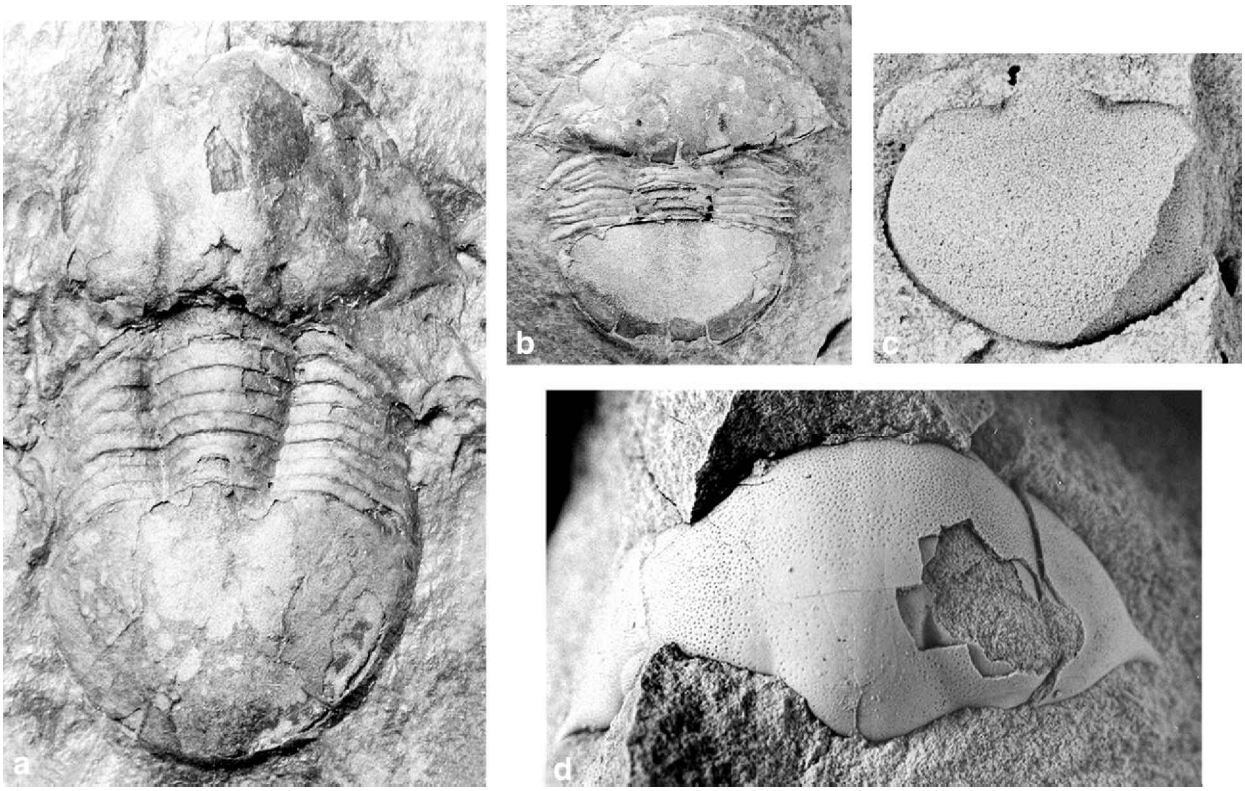

Figure 8 *Octillaenus hisingeri* (Barrande, 1846): (a) complete specimen NM L 15170, lectotype, ×2·1, Králův Dvůr Formation, Králův Dvůr; (b) complete specimen NM L 15169, ×1·6, Králův Dvůr Formation, Králův Dvůr; (d) cephalon NM L 32849, ×3·2, Králův Dvůr Formation, Králův Dvůr-Popovice. *Ectillaenus? holubi* (Šnajdr, 1956); (c) pygidium, holotype, NM L 19265, ×3·1, Libeň, Formation, Rumpál.

non 1980 *Octillaenus hisingeri* (Barrande); Přibyl & Vaněk, pp. 270, 271. (= *Stenopareia oblita*)
1983b *Octillaenus hisingeri* (Barrande); Šnajdr, p. 197.
1989 *Octillaenus hisingeri* (Barrande); Pek & Vaněk, pp. 17, 46.
non 1989 *Octillaenus hisingeri* (Barrande); Pek & Vaněk, p. 46. (= *Stenopareia oblita*)
2000 *Octillaenus hisingeri* (Barrande); Shaw, pp. 375–6, pl. 1, figs 3–5, 7, 14.

Lectotype. Complete specimen NM L15171 from the Králův Dvůr Formation, Králův Dvůr. Figured by Barrande (1852, pl. 29, figs 27, 28). Lectotype designated by Šnajdr (1957).

Other material. Several complete specimens, tens of cephala and pygidia.

Diagnosis. *Octillaenus* species with semicircular cephalon and pygidium, relatively long axial furrows exceeding half the cephalic length in palpebral view. Small eyes situated posteriorly, short genal spines directed downwards.

Description. Vaulted cephalon, semi-circular in outline. Glabella wide, vaulted with distinct axial furrows exceeding half of the cephalic length in palpebral view. Muscle scars of lateral and anterior pairs oval in outline, the basal muscle scars kidney-shaped. Posterior furrows are present in the posterior part of the cephalon, in moulds often observable as keel-shaped elevations.

Facial sutures arched, with small eyes placed near the posterior end of the cephalon at approximately a quarter of the cephalic length in palpebral view. Librigenae triangular in outline, terminating in a blunt genal spine.

Thorax composed of eight segments, the first is longer (tr.) and wider (sag.) than the others. First segment is transversally wider than axis and not so sharply ended as the other thoracic segments.

Pygidium gently vaulted, oval in outline. Lateral margins of pygidium are not as angular as in the other illaenids. Anterior margin slightly rounded, almost straight. Pygidial axis weakly developed, short. Specimens with one and seven axial rings were observed. Pygidial doublure narrow with terrace lines.

Exoskeleton bears a sculpture of dense pits or terrace lines.

Ontogeny. Meraspids with one (NM L 32887, NM L 20413) and two (NM L 33188) unreleased segments on the transitory pygidia are known. They show more parabolic outlines of the cephala and pygidia than do the holaspids. Cephalic axial furrows and pygidial axis well developed, reaching the anterior cephalic and posterior pygidial borders of exoskeleton. Ontogeny of this species was described by Troedsson (1924).

Remarks. Přibyl & Vaněk (1980) and Pek & Vaněk (1989) included *Stenopareia oblita* (Barrande, 1872) in the synonymy of *O. hisingeri* but these taxa apparently represent two separate species.

Bruton & Owen (1988) suggested that *O. hisingeri* developed paedomorphically from *Parillaenus* Jaanusson, 1954, and the restricted number of thoracic segments and smaller size may be the only significant generic-level significance. In this publication *Octillaenus* is maintained as a separate genus, distinguished in having the first thoracic segment longer (tr.) and wider (sag.) than in other illaenids, small eyes located in the most posterior quarter of the cephalic length in palpebral view, and short genal spines.

Occurrence. Králův Dvůr Formation, Czech Republic and Ashgill of Sweden (Troedsson 1924).

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Genus *Zetillaenus* Šnajdr, 1957

Type species. *Illaenus wahlenbergianus* Barrande, 1852 from the Králův Dvůr Formation, Králův Dvůr, Czech Republic.

Remarks. In establishing *Zetillaenus*, Šnajdr (1957) pointed out that it is similar to *Dysplanus* Burmeister, 1843 but differs in having relatively larger eyes, a different course of the axial furrows especially in the posterior part of the cephalon, a shorter pygidial doublure and indistinct pygidial axis. According to Šnajdr (1957), *Dysplanus* has a less vaulted rostral plate and different shape of hypostome.

Jaanusson (1959) placed Šnajdr's genus in the synonymy of *Dysplanus*. Several authors did not ratify this, for example Horný & Bastl (1970) and Šnajdr (1983a). Most recently, Hammann (1992) and Hammann & Leone (1997) discussed the differences between these two genera and considered *Zetillaenus* to be a separate genus. Hammann (1992) had also given a new diagnosis of *Zetillaenus* and a discussion of its validity. Several authors have placed it in the Family Styginidae Vodges, 1890 (e.g. Pek & Vaněk 1989; Hammann 1992). I consider that this genus belongs to the Illaenidae as noted by Whittington (1997). *Zetillaenus* possesses the characteristic ventral ridge in the axial ring of the fulcrate thorax, which is an illaenid feature. *Zetillaenus* differs from *Dysplanus* primarily in having a different course of the axial furrows, which in *Zetillaenus* are shorter and markedly bent, also the rostral plate of *Zetillaenus* has the posterior margin bent upwards, and the pygidium is triangular with indistinct pygidial axis.

Zetillaenus occurs in the Caradoc to Ashgill of the Czech Republic (Šnajdr 1957), Spain (Hammann 1992), Italy (Hammann & Leone 1997) and Burma (Hammann & Leone 1997). In the Czech Republic it is represented only by *Z. wahlenbergianus* (Barrande, 1852).

Zetillaenus wahlenbergianus (Barrande, 1852) (Figs 9a–d, 10a–d)

1846b *Illaenus wahlenbergii* Barrande; Barrande, p. 13.
1847 *Illaenus subtriangularis* nob.; Hawle & Corda, p. 54, pl. 3, fig. 29.
1852 *Illaenus wahlenbergianus* Barrande; Barrande, p. 684, pl. 34, figs 19–25.
1954 *'Illaenus' wahlenbergianus* Barrande; Jaanusson, p. 572.
1957 *Zetillaenus wahlenbergianus* (Barrande); Šnajdr, pp. 170–75, pl. 5, fig. 7; pl. 8, figs 1–5.
1959 *Dysplanus wahlenbergianus* (Barrande); Jaanusson, pp. 139–42.
1970 *Zetillaenus wahlenbergianus* (Barrande); Horný & Bastl, pp. 271, 329, pl. 8, fig. 4.
1983a *Zetillaenus wahlenbergianus* (Barrande); Šnajdr, p. 10, pl. 2, figs 1, 4.
1986 *Zetillaenus wahlenbergianus* (Barrande); Šnajdr, p. 22.
1989 *Zetillaenus wahlenbergianus* (Barrande); Pek & Vaněk, pp. 31.
1992 *Zetillaenus wahlenbergianus* (Barrande); Hammann, pp. 53–4, pl. 3, figs 1–14.
1997 *Zetillaenus wahlenbergianus* (Barrande); Hammann & Leone, pp. 87–8, pl. 15, figs 3, 4, 6–10.
2000 *Zetillaenus wahlenbergianus* (Barrande); Shaw, p. 377, pl. 1, figs 16–21.

Lectotype. Complete specimen NM L15261 figured by Barrande (1852, pl. 34, figs 20–22) from the Králův Dvůr Formation, Králův Dvůr. Lectotype designated by Šnajdr (1957).

Other material. Tens of complete and enrolled specimens, cephala and pygidia.

Diagnosis. *Zetillaenus* species with parabolic cephalon and pygidium, axial furrows reaching maximally half the length of the cephalon. Triangular librigenae extending into short genal spines, pygidial axis weakly distinct.

Description. Cephalon parabolic and vaulted, especially the glabella where a keel-like mesial elevation is present in some specimens. Axial furrows occupy half the cephalic length in palpebral view; older holaspids possess shorter axial furrows. Posterior furrows, medial tubercle and occipital ring are present.

Lateral and occipital muscle scars oval, basal scars kidney-shaped. Facial suture curved in first third of its length in palpebral view. Librigenae small, triangular, extending into short genal spines directed posteriorly.

Anterior margin of hypostome slightly arched, middle hypostomal lobe with terrace lines, rostral plate wide, trapezoidal in outline with parabolic anterior margin, posterior margin bent upwards. Surface sculpture of terrace lines parallel with the anterior margin of cephalon.

Thorax consisting of nine thoracic segments. Axis is widest in the anterior part and narrows (moderately) posteriorly to two-thirds of its width. The pleurae show a proportional increase in width as the axis tapers but the whole thorax does not.

Compared with the cephalon, the pygidium is smaller, vaulted and triangular in outline with parabolic posterior margin. Pygidial axis indistinct and short, reaching one-third of the pygidial length in dorsal view. Pygidial doublure narrow, smooth, bearing terrace lines parallel with the posterior margin.

Sculpture of exoskeleton composed of dense pitting and terrace lines.

Specimens of *Z. wahlenbergianus* are often found sphaeroidally enrolled with cephala and pygidia in close contact and librigenae covering the lateral ends of the pleurae.

Ontogeny. Several meraspids with one (NM L 33189, NM L 20412, NM L 32867, NM L 33182), three (NM L 32863, NM L 32864, NM L 33195), four (NM L 20415, NM L 33040), five (NM L 33183, NM L 33187) and seven (NM L 32895) unreleased segments on the transitory pygidia were observed. The last specimen shows the first three thoracic segments clearly distinct in the anterior part of the pygidium; the last one is only weakly perceptible. Pygidia and cephala (NM L 32883, NM L 33882) of meraspids show less parabolic outlines than in holaspids. Axial furrows and pygidial axis distinct and long.

Remarks. Barrande (1846b) mentioned *Illaenus Wahlenbergi* in a faunal list and in 1852 he changed the specific name to *Illaenus Wahlenbergianus*, and included *Illaenus subtriangularis* Hawle & Corda, 1847 in its synonymy. According to the rule of priority, *Illaenus subtriangularis* should strictly be valid. However this would disturb the stability of nomenclature of a well-understood taxon and I recommend that the present usage be maintained.

Zetillaenus ibericus Hammann, 1976 from the Sardinian Upper Ordovician possesses semicircular and wider (tr.) cephala and pygidia, wider (tr.) glabella. This taxon differs from other Bohemian illaenids in having a parabolic outline of cephalon and pygidium, short genal spines directed obliquely backwards, and small eyes situated in the posterior part of the cephalon. Short and indistinct pygidial axis reaching one-third of the length of the pygidium in dorsal view.

Occurrence. Králův Dvůr Formation, Czech Republic and Ashgill of Spain (Hammann 1992) and Italy (Hammann & Leone 1997).

Genus *Stenopareia* Holm, 1886

Type species. *Illaenus linnarssoni* Holm, 1882 from the Boda Limestone (Ashgill), Dalarna, Sweden.

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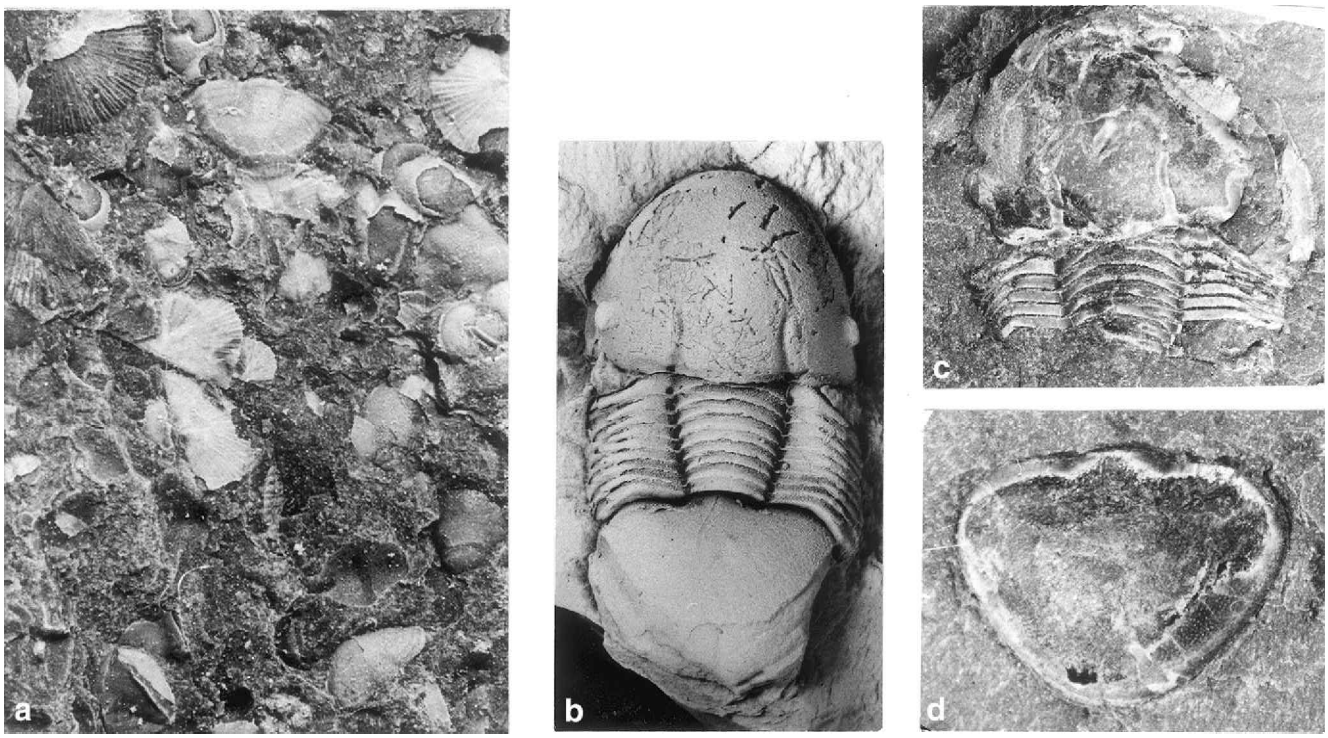

Figure 9 *Zetillaenus wahlenbergianus* (Barrande, 1852): (a) pygidia of two meraspid specimens NM L 33040, ×10, Králův Dvůr Formation, Levín; (b) complete specimen NM L 32898, ×2.5, Králův Dvůr Formation, Lejškov; (c) incomplete cephalon and thorax L 33045, unwhitened specimen, ×3.5, Králův Dvůr Formation, Levín; (d) pygidium NM L 33045, unwhitened specimen, ×3.5, Králův Dvůr Formation, Levín.

Remarks. Although *Stenopareia* was established by Holm in 1886, palaeontologists used the designation *Illaenus* Dalman, 1827, for many species now ascribed to that genus until Jaanusson (1954) and Šnajdr (1956, 1957) applied Holm's generic determination.

In 1997 Vaněk & Vokáč established the new genus *Vysocania*, with type species *V. vaneki* (Šnajdr, 1958). This genus is here considered as a junior synonym of *Stenopareia* (*see* remarks to *S. vaneki*). *S. vaneki* was placed in *Ulugtella* Petrunina, 1975 by some authors (e.g. Hammann 1992). I still consider this species as the representative of *Stenopareia* even if it probably lacks the eyes, the typical feature of *Stenopareia* species. *S. vaneki* is distinguished from *Ulugtella* by its slightly curved facial suture, although in the poor material studied no eyes were observed. Glabella of *S. vaneki* is wider (tr.) with shorter axial furrows, conversely pygidium is shorter (tr.).

Stenopareia occurs from the Caradoc to Wenlock of the Czech Republic (Šnajdr 1956, 1957), Norway (Owen & Bruton 1980; Bruton & Owen 1988), Sweden (Owen & Bruton 1980), Scotland (Howells 1982; Whittington 1997), Wales (see Hammann 1992), England (Whittard 1956; Morris 1988; Curtis & Lane 1997), Kazakhstan (see Hammann 1992). In Bohemia it is represented by *S.*? *hospes* (Barrande, 1872), *S. oblita* (Barrande, 1872), *S. panderi* (Barrande, 1852) and *S. vaneki* (Šnajdr, 1958).

Stenopareia panderi (Barrande, 1852)
(Fig. 11a–c)

1846a *Illaenus crassicauda* Wahlenberg; Barrande, p. 33.
1847 *Illaenus laticeps* nob.; Hawle & Corda, p. 54.
1847 *Illaenus attenuatus* nob.; Hawle & Corda, p. 54.
1852 *Illaenus panderi* Barrande; Barrande, p. 682, pl. 30, fig. 18.
1852 *Illaenus salteri* Barrande; Barrande, p. 682, pl. 35, fig. 18.
non 1852 *Illaenus panderi* Barrande; Barrande, pl. 30, figs 10, 11. (= *Stenopareia oblita*).
1872 *Homalonotus minor* Barrande; Barrande, p. 39, pl. 14, fig. 29.
1886 *Stenopareia panderi* (Barrande); Holm, p. 152.
1954 *Stenopareia panderi* (Barrande); Jaanusson, p. 570.
1956 *Stenopareia panderi* (Barrande); Šnajdr, pp. 496–9, pl. 1, fig. 4.
1957 *Stenopareia panderi* (Barrande); Šnajdr, pp. 160–6, pl. 7, figs 3–7.
1970 *Stenopareia panderi* (Barrande); Horný & Bastl, pp. 200, 231, 232, 275.
1976 *Stenopareia panderi* (Barrande); Přibyl & Vaněk, pp. 18, 23.
1983b *Stenopareia panderi* (Barrande); Šnajdr, p. 139.
1988 *Ectillaenus holubi* (Šnajdr); Moravec, p. 344, pl. 1, figs 1–5.
1989 *Stenopareia panderi* (Barrande); Pek & Vaněk, pp. 18, 35, 43.
1997 *Vysocania vaneki* (Šnajdr); Vaněk & Vokáč, pl. 2, figs 12–13, 15–16.

Lectotype. Complete specimen NM L 15607, figured by Barrande (1852, pl. 35, fig. 21) from the Zahořany Formation at Zahořany. Lectotype designated by Šnajdr (1957).

Other material. About 20 complete specimens (several of them enrolled), hundreds of isolated cephala and pygidia.

Diagnosis. *Stenopareia* species with an oval cephalon, and semicircular anterior border of cephalon. Pygidium smaller than cephalon, wide and oval in outline with rounded lateral borders, and vaulted especially postaxially.

Description. Cephalon strongly vaulted (especially glabella), oval in outline and semicircular in its anterior part. Axial furrows arched, occupying maximally the first half of the cephalic length in palpebral view. Younger specimens show

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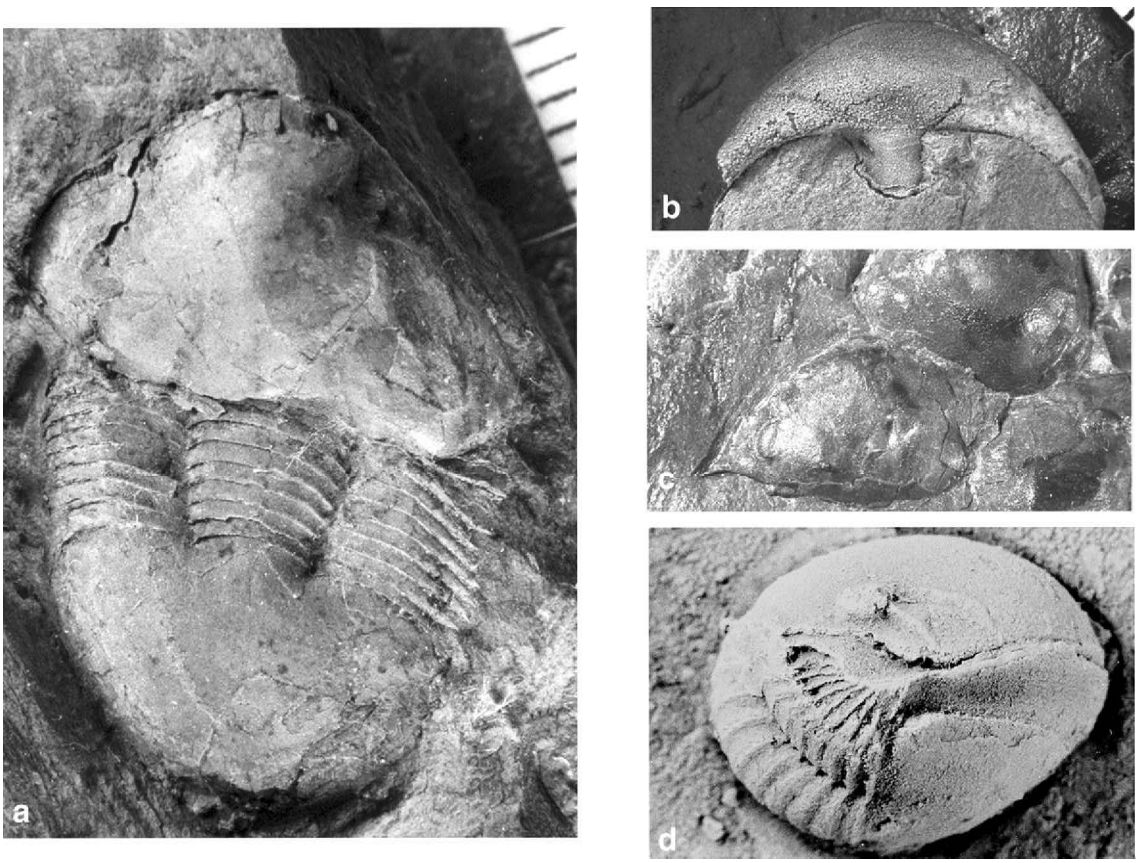

Figure 10 *Zetillaenus wahlenbergianus* (Barrande, 1852): (a) complete specimen, unwhitened specimen, lectotype, NM L 15261, ×5·5, Králův Dvůr Formation, Králův Dvůr; (b) enrolled specimen with rostrum and hypostome *in situ* CGU MŠ 745, ×5, Králův Dvůr Formation, Králův Dvůr-Ovčín; (c) cephalon NM L 36010, unwhitened specimen, ×2·6, Králův Dvůr Formation, Levín; (d) enrolled specimen NM L 33046, ×4, Králův Dvůr Formation, Lejškov.

more distinct and longer axial furrows. Outside the arch of furrows lateral muscle scars, oval in outline, are developed. Occipital muscle scars circular, the basal scar is kidney-shaped, the middle and anterior scars oval in outline.

Facial suture moderately strongly bent outwards at the level of palpebral lobes. Relatively small eyes located near the posterior margin of cephalon and composed of approximately 200 lenses. Librigenae narrow, laterally curved, without genal spines.

Rostral plate trapezoidal in outline, narrow, bearing terrace lines parallel with the anterior margin of cephalon. Middle hypostomal lobe sculpted with terrace lines. Anterior margin of hypostome slightly arched.

Thorax consisting of nine thoracic segments. Axis is widest at the level of the second and third thoracic segments and narrows posteriorly.

Pygidium smaller than cephalon, wide and oval in outline, with suboval posterior margin and vaulted especially post-axially. Lateral margins of pygidium arched posteriorly. Pygidial axis weakly developed and short. Doublure bearing wavy terrace lines parallel with the posterior margin of pygidium; it is widest mesially where (in dorsal view) it occupies one-third of the pygidial length.

Sculpture consists of dense pitting combined with terrace lines.

Ontogeny. One cephalic shield (NM L 33193) of a probable meraspid or young holaspid specimen was found. Cephalon suboval in outline with very distinct long axial furrows. Pygidia of young holaspids are oval in outline and on the lateral margins are less steeply angled than in the older holaspids.

Remarks. The material subsequently ascribed to *S. panderi* was first mentioned by Barrande (1846b) as *Illaenus crassicauda* Wahlenberg. Hawle & Corda (1847) established *Illaenus attenuatus* and *Illaenus laticeps* which were synonymised by Barrande (1852) with his new species *Illaenus panderi*. All subsequent authors have used Barrande's (1852) denomination. Šnajdr (1957) discussed the validity of *S. panderi* and inclined to the usage of Barrande's (1852) species because he figured and described it better than did Hawle & Corda (1847). This step is also in accordance with the rules of nomenclature since the application of the principle of priority could affect the stability of discussed species.

Vaněk & Vokáč (1997) considered that the specimens of *S. panderi* occurring in the Bohdalec Formation belong in *Stenopareia* (their: *Vysocania*). However, the material of *S. panderi* from the Bohdalec Formation is here reassigned to Barrande's species. *S. vaneki* has a more rounded outline of the anterior part of the cephalon, and the anterior borders of this pygidium are straight and wider (tr.) than in *S. panderi* (*S. vaneki* is discussed below).

Type species *S. linnarssoni* (Holm, 1882) possesses wider (tr.) glabella with longer and not so outwardly curved axial furrows (as in *S. panderi*), larger eyes situated on swollen palpebral lobes and semicircular pygidium. It is distinguished from another common Scandinavian species *S. glaber* (Kjerulf, 1865) by, for example, the different shape of its hypostome and rostral plate. In *S. panderi* the hypostome possesses a semicircular posterior border and steeply inclined middle furrow; the rostral plate is widely trapezoidal. *S. panderi* differs from Bohemian *Stenopareia* species in having wider (tr.) cephala

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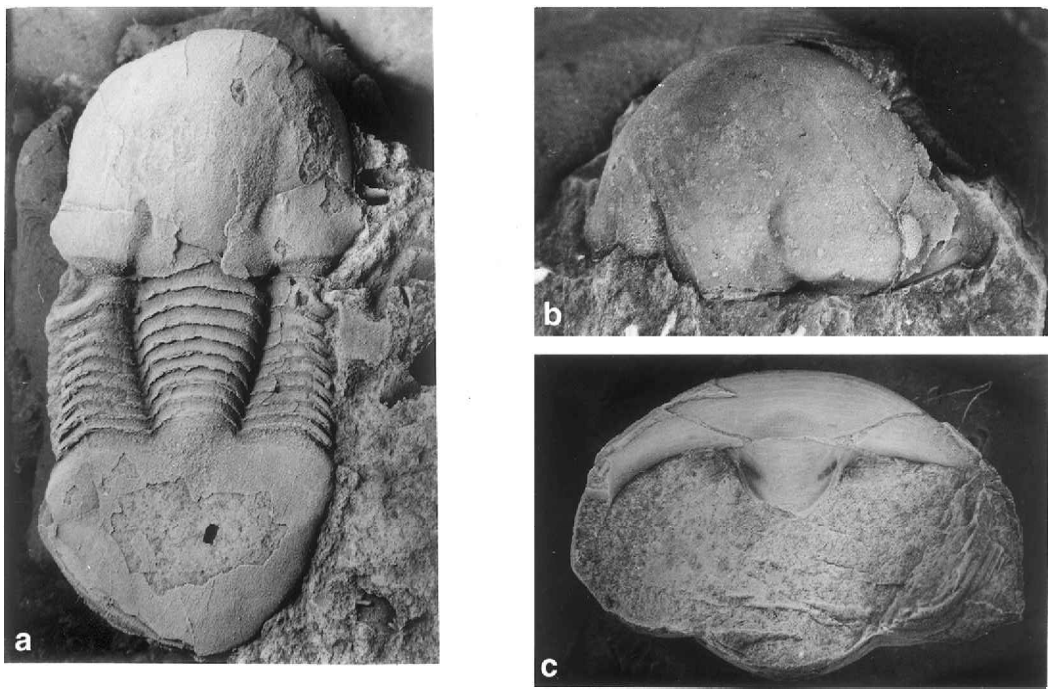

Figure 11 *Stenopareia panderi* (Barrande, 1852): (a) almost complete specimen, lectotype, NM L 15607, ×2·5, Zahořany Formation, Zahořany; (b) cephalon CGU JV 2290, ×3·7, Vinice Formation, Nučice; (c) enrolled specimen with rostrum and hypostome *in situ* CGU MŠ 21, ×3, Zahořany Formation, Loděnice-Kněžská hora.

and pygidia, with gently arched posterior margins of the pygidium.

Ontogeny. Cephala of probable meraspid specimens are semicircular in outline with long and easily observable axial furrows. Pygidia oval, laterally less vaulted than in the holaspid specimens.

Occurrence. Libeň to Bohdalec formations, Czech Republic.

Stenopareia oblita (Barrande, 1872)
(Fig. 12a–e)

1852 *Illaenus panderi* Barrande; Barrande, pl. 30, figs 10, 11.
1872 *Illaenus oblitus* Barrande; Barrande, p. 73, pl. 15, figs 44, 45.
non 1872 *Illaenus oblitus* Barrande; Barrande, pl. 15, figs 42, 43. (= *Lichas rudis*)
1957 *Stenopareia oblita* (Barrande); Šnajdr, pp. 166–9, pl. 7, figs 8–10.
1970 *Stenopareia oblita* (Barrande); Horný & Bastl, pp. 220, 231, 232.
1980 *Octillaenus hisingeri* (Barrande) [pars]; Přibyl & Vaněk, pp. 270, 271, pl. 2, fig.5.
1989 *Octillaenus hisingeri* (Barrande) [pars]; Pek & Vaněk, p. 46.
2000 *Stenopareia oblita* (Barrande); Shaw, pp. 376–7, pl. 1, figs 9–13, 15.

Lectotype. Incomplete cranidium NM L 16974 from the Králův Dvůr Formation, Kosov, Barrande (1872, pl. 15, figs 44, 45). Lectotype derived by Šnajdr (1957).

Other material. Tens of cranidia, pygidia, one damaged specimen and incomplete cephalon, thorax. Only one specimen with incomplete (tr.) wide librigenae was observed.

Diagnosis. *Stenopareia* species with semicircular cephalon. Axial furrows extending two-thirds of the cephalic length in palpebral view. Pygidium oval with semicircular posterior margin.

Ontogeny. Meraspid pygidia with one (CGU RŠ 345, CGU RŠ 395, CGU RŠ 418, CGU RŠ 360, CGU RŠ 475), two (CGU RŠ 404, CGU JV 2743 a), three (CGU RŠ 435), and four (CGU JV 2743 a) unreleased segments on the transitory pygidia were observed. Pygidia oval in outline and more longer (tr.) than in the holaspids.

Remarks. *S. oblita* was originally figured by Barrande (1852) within material assigned to *I. panderi* before the species was described 20 years later (1872). Přibyl & Vaněk (1980) and Pek & Vaněk (1989) considered it to be a synonym of *Octillaenus hisingeri* (Barrande, 1846). But in *Octillaenus hisingeri* the pygidium is typically transversely longer and the cephalon narrower with shorter axial furrows.

In contrast to the type species, *S. oblita* has a narrower (tr.) glabella, bent axial furrows and less semicircular pygidium.

Occurrence. Králův Dvůr Formation where it belongs to the most common fossil remains of the 'Perník Beds' (*Proboscisambon* Community, *see* Marek 1952; Chlupáč 1953) in the upper part of this formation. *S. oblita* is found also in the dark grey shales of the upper Králův Dvůr Formation, Czech Republic.

Stenopareia vaneki (Šnajdr, 1958)
(Fig. 12f–i)

1957 *Zbirovia vaněki* nov. sp.; Šnajdr, p. 193.
1958 *Zbirovia vaněki*; Šnajdr, pp. 207–11, text figs 1, 2, pl. 2, figs 10–20.
1989 *Stenopareia vaneki* (Šnajdr); Pek & Vaněk, p. 18.
1992 ?*Ulugtella vaneki* (Šnajdr); Hammann, p. 76.
1997 *Vysocania vaneki* (Šnajdr); Vaněk & Vokáč, pp. 22, 27, 28, pl. 2, figs 14, 17–21.
non 1997 *Vysocania vaneki* (Šnajdr); Vaněk & Vokáč, pl. 2, figs 12–13, 15–16. (= *S. panderi*)

Holotype. Pygidium NM L 17619 figured by Šnajdr (1958, pl. 2, fig. 16) from the Bohdalec Formation (Karlík Iron Ore Horizon at the base of this formation) at Praha-Hloubětín.

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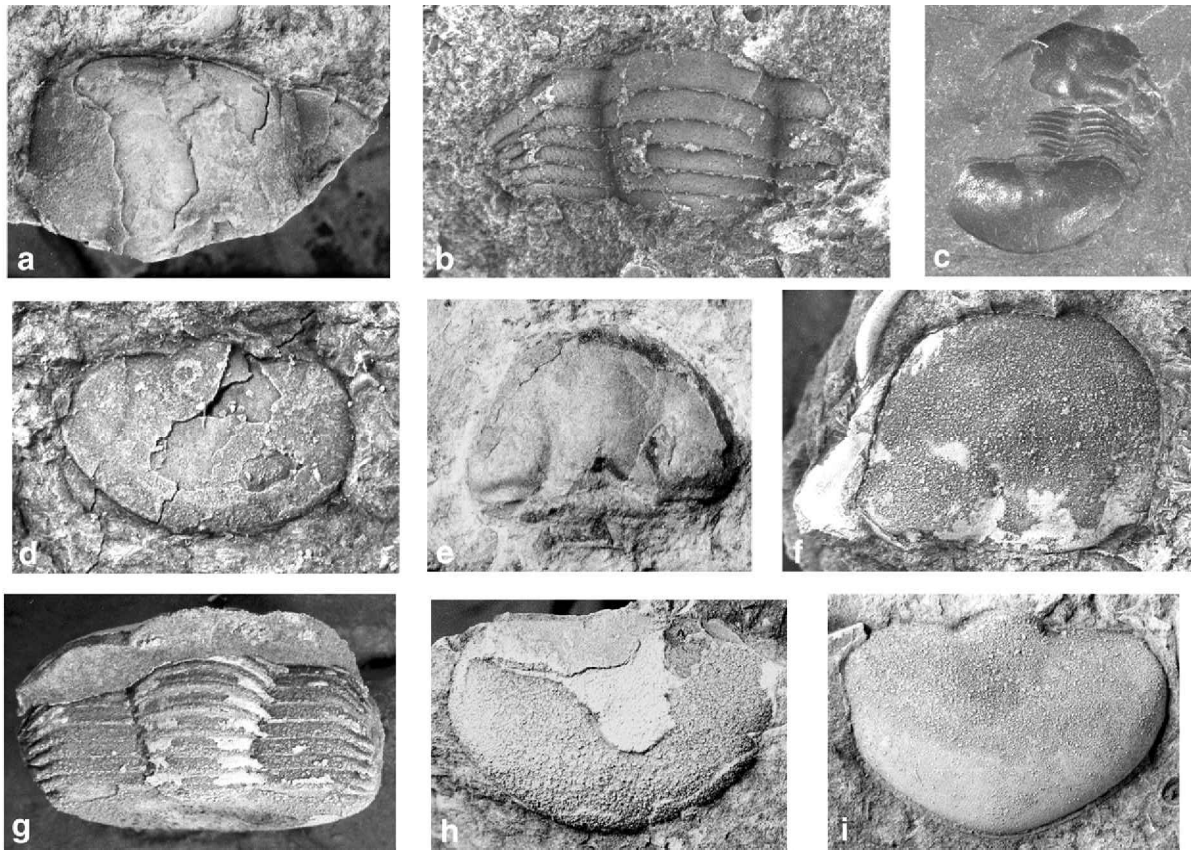

Figure 12 *Stenopareia oblita* (Barrande, 1872): (a) incomplete cephalon CGU JV 1521, ×3, Králův Dvůr Formation, Zadní Třebáň; (b) incomplete thorax CGU MM 237, ×4·6, Králův Dvůr Formation, Libomyšl; (c) incomplete specimen, unwhitened specimen, CGU JH 5163, ×4, Králův Dvůr Formation, Praha-Pankrác; (d) pygidium NM L 36011, ×5, Králův Dvůr Formation, Zadní Třebáň; (e) cranidium, unwhitened specimen, lectotype, NM L 16974, ×3·5, Králův Dvůr Formation, Kosov. *Stenopareia vaneki* (Šnajdr, 1958); (f) incomplete cephalon CGU MŠ 3, ×3·6, Bohdalec Formation, Praha-Hloubětín; (g) thorax CGU JV 2295, ×5, Bohdalec Formation, Praha-Hloubětín; (h) pygidium NM L 33056, ×3.8, Bohdalec Formation, Praha-Hloubětín; (i) pygidium, holotype, NM L 17619, ×3·4, Bohdalec Formation, Praha-Hloubětín.

Other material. Tens of cephalic (mostly cranidia) and pygidial shields, several enrolled specimens.

Diagnosis. Species of *Stenopareia* with semicircular anterior part of cephalon, almost straight facial suture, probably with no eyes. Pygidium oval with straight, transversally long anterior margins and steeply sloped lateral margins.

Remarks. In the revision of illaenid trilobites Šnajdr (1957) mentioned that he recognised a new species *Zbirovia vaneki* nov. sp. but this species only became valid when it was first described and figured in 1958. Pek & Vaněk (1989) assigned this taxon to *Stenopareia* Holm, 1886 and but Hammann (1992) suggested it might belong in *Ulugtella* Petrunina, 1975.

As is noted in the genus discussion, Vaněk & Vokáč (1997) defined a new genus *Vysocania* with a type species *Z. vaneki* but this genus is here considered as a junior synonym of *Stenopareia*. Vaněk & Vokáč (1997) also presented illustrations of their new genus, but several of these figured specimens are actually *S. panderi*.

Stenopareia vaneki differs from the type species *S. linnarssoni* (Jaanusson 1954; Owen & Bruton 1980; Bruton & Owen 1988) in having a longer (tr.), probably blind cephalon with an almost straight facial suture, axial furrows curved more outwardly and pygidium oval, having a straight anterior margin with obliquely sloping lateral margins. From other Bohemian and/or outside *Stenopareia* species it may be distinguished by its probable blindness, wide pygidium (tr.) with straight anterior margin and sloping lateral margins.

From *Zbirovia arata* as the type species of the genus to which it was previously ranged, it differs in having wider (tr.) glabella, and upwardly bent posterior margin of the cephalon, in contrast to that of *Z. arata* which is bent downwards. Thorax of this species possesses nine thoracic segments, pygidium is wider (tr.) with less steeply cut lateral borders.

Occurrence. Karlík Iron Ore Horizon at the base of the Bohdalec Formation, Czech Republic.

Stenopareia? *hospes* (Barrande, 1872)
(Fig. 13a–b)

1872 *Illaenus hospes* Barrande; Barrande, pl. 2, figs 13–15.
1957 *'Illaenus' hospes* Barrande; Šnajdr, p. 246.
1957 *Ectillaenus* sp.; Šnajdr, p. 224, pl. 5, fig. 9.
1970 *'Illaenus' hospes* Barrande; Horný & Bastl, p. 169.
1989 *Stenopareia* (?) *hospes* (Barrande); Pek & Vaněk, p. 18.
2000 *Illaenus hospes* (Barrande); Shaw, p. 376, pl. 1, fig. 8.

Lectotype. Incomplete specimen NM L 16623 figured by Barrande (1872, pl. 2, figs 13–15) from the Králův Dvůr Formation at Králův Dvůr. Lectotype designated by Šnajdr (1957).

Other material. Four cranidia, two parts of thorax, six pygidia.

Diagnosis. Cephalon and glabella wide (tr.), with axial furrows reaching half of the cephalic length, in palpebral view, ?nine thoracic segments, pygidium oval, wide (tr.) with rounded

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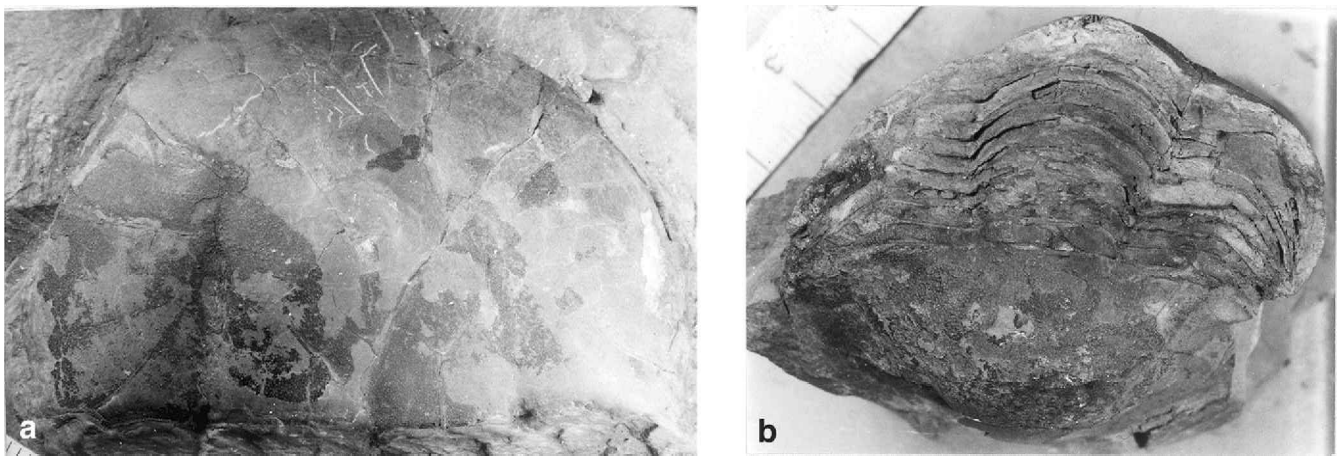

Figure 13 *Stenopareid? hospes* (Barrande, 1872), specimens unwhitened: (a) cranidium NM L 19275, ×1·5, Králův Dvůr Formation, Králův Dvůr; (b) pygidium with incomplete thorax, lectotype, NM L 16623, ×1·1, Králův Dvůr Formation, Lejškov.

anterior margins and wide doublure reaching half of pygidial length, in dorsal view.

Remarks. Pek & Vaněk (1989) placed this species in *Stenopareia*. The outline of the pygidium resembles that of *Stenopareia* but the gross morphology of the cephalic shield is close to *Ectillaenus* Salter, 1867. It is possible, as at first mentioned by Šnajdr (1957), that it represents a new genus.

This species is distinguished from other illaenid species by its large dimensions (sagittal length of cephalon 38 mm, pygidium 36 mm), wide glabella and pygidial doublure (tr.) reaching half of the pygidial length in dorsal view. It differs from the type species of *Illaenus* Dalman, 1827, '*I. crassicauda*', in having a narrower (tr.) cephalon, probably no eyes, and a different shape of glabellar furrows. *S.? hospes* resembles *S. panderi* but it seems that this species had no eyes, wider glabella with less outwardly curved axial furrows, indistinct pygidial axis and very wide pygidial doublure (see above). The exact determination of this taxon requires new discoveries of more complete and better-preserved specimens.

Occurrence. Králův Dvůr Formation, Czech Republic.

Genus *Cekovia* Šnajdr, 1956

Type species. *Illaenus transfuga* Barrande, 1852 from the Letná Formation at Děd hill near Beroun, Czech Republic.

Remarks. Hammann (1992) discussed Šnajdŕs (1957) generic analysis of this taxon and considered the group of blind *Cekovia* species as belonging to *Ulugtella* Petrunina, 1975. In my opinion, the blind species *C. goetz*i belongs to *Cekovia* (see the remarks to this species). *Cekovia* differs from other illaenids in having a strongly swollen cephalon, especially the glabella, distinct and long axial furrows, eyes situated posteriorly, 10 thoracic segments and pygidium with a semicircular posterior margin.

Cekovia is found in the Caradoc and Ashgill of the Czech Republic (Šnajdr 1956; Šnajdr 1957), Spain (Hammann 1992), France (*see* Hammann 1992), Germany (*see* Hammann 1992) and China (*see* Hammann 1992). In Bohemia it is represented by *C. transfuga* (Barrande, 1852), *C. salteri* (Barrande, 1872) and *C. goetzi* Šnajdr, 1956.

Cekovia transfuga (Barrande, 1852)
(Fig. 14e–g)

1852 *Illaenus transfuga* Barrande; Barrande, p. 688, pl. 30, fig.1.

non 1852 *Illaenus transfuga* Barrande; Barrande, pl. 30, fig. 3. (= *Cekovia salteri*)

1956 *Cekovia transfuga* (Barrande); Šnajdr, pp. 493–5, pl. 2, figs 1–4.

1957 *Cekovia transfuga* (Barrande); Šnajdr, pp. 176–9, pl. 5, fig. 8, pl. 8, figs 6–12, pl. 9, fig. 2.

1970 *Cekovia transfuga* (Barrande); Horný & Bastl, pp. 310, 311, pl. 8, fig. 2.

1989 *Cekovia transfuga* (Barrande); Pek & Vaněk, pp. 17, 47.

Lectotype. Incomplete pygidium NM L15179 figured by Barrande (1852, pl. 30, figs 1, 2) from the Letná Formation at Děd hill near Beroun. Lectotype designated by Šnajdr (1957).

Other material. Several tens of cephala and pygidia.

Diagnosis. Representative of *Cekovia* with distinct, long axial furrows reaching the anterior margin of the cephalon. Pygidium wide (tr.) with a rounded posterior margin, anterior margin bent downwards and sharply cut lateral borders.

Description. Cephalon vaulted, strongly in its middle part, semicircular in outline. A narrow flat margin is developed in the anterior part of the cephalon. Outwardly curved axial furrows well pronounced, extending to the anterior margin of cephalon, becoming shallower anteriorly. Occipital, basal, middle and anterior pairs of glabellar muscle scars are circular, the lateral pair being crescentic in outline. Facial suture almost straight and curved inwardly behind eyes. Posterior part of fixigenae with moderate curve. Librigenae triangular in outline with rounded lateral margins. Eyes on elevated palpebral lobes, which are located in the posterior third of the length (sag.) of cephalon.

Rostral plate and hypostome unknown.

Thorax unknown.

Pygidium wide (tr.), vaulted with a rounded posterior margin, anterior margin bent downwards and sharply cut lateral borders.

Sculpture composed of dense pitting.

Ontogeny. Several indeterminable cephala of probably very young holaspid specimens of *Cekovia* sp. are known from the Letná Formation. Cephala parabolic in outline and vaulted; in the anterior direction it passes into a narrow margin. Glabella more strongly vaulted than the fixigenae, palpebral lobes swollen.

Remarks. According to Šnajdr (1957) this species possesses a thorax with 10 segments, unfortunately in the course of this

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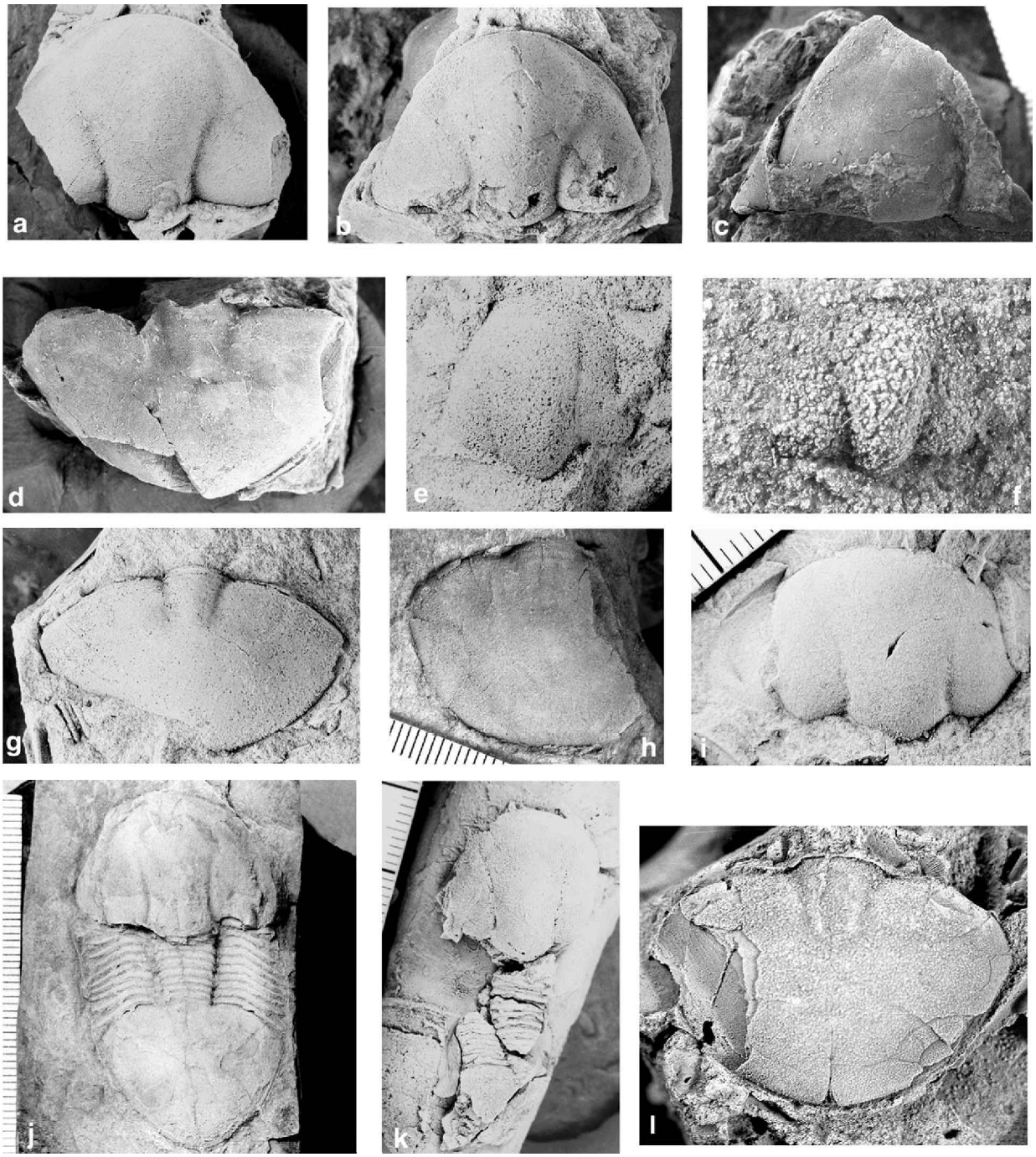

Figure 14 *Cekovia goetzi* Šnajdr, 1957: (a) cranidium NM L 33048, ×1·8, Vinice Formation, Chrustenice; (b) cranidium, holotype, NM L 19282, ×1·7, Vinice Formation, Chrustenice; (c) incomplete cephalon CGU MŠ 29, ×1·6, Vinice Formation, Chrustenice; (d) pygidium NM L 36058, ×2·9, Vinice Formation, Chrustenice. *Cekovia transfuga* (Barrande, 1852); (e) cranidium NM L 33052, ×3·5, Letná Formation, Drabov; (f) cranidium of young specimen NM L 32925, ×12·5, Letná Formation, Drabov; (g) pygidium, lectotype, NM L 15179, ×1·9, Letná Formation, Drabov. *Cekovia salteri* (Barrande, 1872); (h) incomplete pygidium CGU VH 5111, ×1·5, Zahořany, Praha-Spořilov; (i) cephalon NM L 33050, ×1·8, Zahořany Formation, Praha-Bohdalec; (j) incomplete specimen, lectotype, NM L 15299, ×1·3, Zahořany Formation, Zahořany; (k) incomplete specimen on the shell of an orthocone cephalopod NM L 32931, ×1·5, Vinice Formation, Chrustenice; (l) pygidium CHU 360, ×2·4, Zahořany Formation, Zahořany.

revision no specimen with an intact thorax was found. Another Bohemian *Cekovia* species *C. goetzi* possesses no eyes, genal spines, or distinct pygidial axis with laterally swollen parts. The anterior border of *C. transfuga* is bent downwards; in contrast it is straighter in *C. goetzi*. *C. perplexa* Hammann, 1992 from the Ashgill of Spain has a wider glabella in its anterior part with more outwardly curved axial furrows and a narrower (tr.) pygidium. *C. ?munieri* Kerforne, 1900 from the Upper Ordovician of Spain described by Hammann (1992), is distinguished also in having short genal spines directed backwards, anteriorly wider glabella and strongly outwardly curved axial furrows.

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Occurrence. Libeň and Letná formations.

Cekovia salteri (Barrande, 1852)
(Fig. 14h–l)

1847 *Illaenus limbatus* nob.; Hawle & Corda, p. 54.
1852 *Illaenus salteri* Barrande; Barrande, p. 685, pl. 35, figs 9–17, 19, 20.
1852 *Illaenus transfuga* Barrande [pars]; Barrande, pl. 30, fig. 3.
non 1852 *Illaenus salteri* Barrande; Barrande, p. 682, pl. 35, fig. 18. (= *Stenopareia panderi*)
1852 *Illaenus distinctus* Barrande; Barrande, p. 687, pl. 29, figs 23, 24.
1954 *Illaenus salteri* Barrande; Jaanusson, p. 576.
1956 *Cekovia salteri* (Barrande); Šnajdr, p. 493.
1957 *Cekovia salteri* (Barrande); Šnajdr, pp. 179–83, pl. 9, fig. 1.
1970 *Cekovia salteri* (Barrande); Horný & Bastl, pp. 121, 189, 275, 311.
1989 *Cekovia salteri* (Barrande); Pek & Vaněk, pp. 17, 39.

Lectotype. Complete specimen NM L15299 from the Zahořany Formation at Zahořany. Figured by Barrande (1852, pl. 35, fig. 11). Lectotype designated by Šnajdr (1957).

Other material. Several complete specimens, tens of cephala (mostly cranidia) and pygidia.

Diagnosis. A species of *Cekovia* with semicircular vaulted cephalon, wider (tr.) than in the type species. Axial furrows distinct, long, but not reaching the anterior part of cephalon. Pygidium semicircular in outline, with widely rounded lateral borders.

Remarks. Hawle & Corda (1847) originally described *Illaenus limbatus* which is identical with Barrande's (1852) *I. salteri*. Although the species designation of Hawle & Corda (1847) has historical priority, it was neglected for more than 100 years. Šnajdr (1957) noted that *I. salteri* is a widely used species name and that the principle of priority could break the stability of this taxon, therefore the mode of usage is retained.

The most similar species to *C. salteri* is *C. transfuga*; the former taxon differs from it in having shorter axial furrows which do not reach the anterior margin of the cephalon and longer (sag.) pygidium with less sharply cut lateral borders. A close relationship exists between these two species and as Šnajdr (1957) suggested *C. salteri* is probably a descendant of *C. transfuga*.

Occurrence. Vinice and Zahořany formations, Czech Republic. Knüpfer (1967) mentioned it from the lower Ashgill of Thuringia.

Cekovia goetzi Šnajdr, 1957
(Fig. 14a–d)

Illaenus götzi; Novák, unpublished manuscript
1957 *Cekovia götzi* nov. sp.; Šnajdr, pp. 183–7, pl. 5, fig. 10, pl. 6, figs 3–9.
1970 *Cekovia götzi* Šnajdr; Horný & Bastl, p. 154.
1989 *Ulugtella goetzi* (Šnajdr); Pek & Vaněk, p. 18.
1997 *Ulugtella goetzi* (Šnajdr); Vaněk & Vokáč, p. 28.

Holotype. Cephalon NM L 19282 from the Vinice Formation (Nučice Iron Ore Horizon at the base of this formation) at Chrustenice mine, Štětka. Figured by Šnajdr (1957, pl. 9, fig. 3).

Other material. About 20 cephalic shields and pygidia.

Diagnosis. Blind *Cekovia* species with parabolic, strongly vaulted cephalon, narrow (tr.) clavate glabella, expanding strongly anteriorly and robust genal spines. Pygidium parabolic in outline with low swollen mounds in its anterior part, axis distinct.

Ontogeny. One specimen (CGU VH 5176) with five unreleased segments on the transitory pygidia was studied. Pygidium oval in outline.

Remarks. *Illaenus götzi* was originally named by Novák (undated) in an unpublished manuscript without a description. Šnajdr (1957) subsequently described and figured it.

Pek & Vaněk (1989), Hammann (1992) and Hammann & Leone (1997) assigned this species to *Ulugtella* Petrunina, 1975. It is here placed in *Cekovia* and distinguished from *Ulugtella* by longer axial furrows which in adults of *Ulugtella* do not reach the anterior margin, and narrower (tr.) glabella, almost twice as narrow as the fixigenae and librigenae and terminating in genal spines. *Ulugtella* has a glabella as wide as or narrower than the fixigenae and very small librigenae, it also possesses a semi-elliptical pygidium outline in contrast to the parabolic pygidium of *C. goetzi*. According to Šnajdr (1957) *C. goetzi* possesses ten thoracic segments while *Ulugtella* has probably only nine. Šnajdr (1957) described a damaged specimen with ten thoracic segments but in the course of the present study this specimen was not found.

It differs from other Bohemian species in having no eyes, narrow (tr.) glabella (almost styginid-like) and parabolic outlines of cephalon and pygidium. Axial furrows are strongly curved outwards in the posterior part of the cephalon and in the anterior part curved inwardly. Glabella is strongly vaulted in its middle part. Pygidium with distinct axis and two low swollen mounds in its anterior part. *C. goetzi* probably originated from *C. salteri* in the specific conditions of the Nučice Iron Ore Horizon of the Vinice Formation.

Occurrence. Nučice Iron Ore Horizon at the base of the Vinice Formation, Czech Republic.

Genus *Zbirovia* Šnajdr, 1956

Type species. *Illaenus aratus* Barrande, 1872 from the Dobrotivá Formation at St. Dobrotivá, Czech Republic.

Remarks. A diagnosis of *Zbirovia* was given by Šnajdr (1956, 1957) who established this genus. Dean & Monod (1990) considered that *Zbirovia* belongs to a group of illaenid trilobites (together with *Alceste* Hawle et Corda, 1847, *Zdicella* Šnajdr, 1956 and *Ulugtella* Petrunina, 1975), which can be distinguished only on the basis of their pygidia and are in need of revision. Hammann (1992), however, acknowledged the validity of *Zbirovia* and discussed the attribution of species to that genus.

Zbirovia is distinguished from *Alceste* by its shorter, less distinct and more outwardly curved axial furrows and different outline of the pygidium, which is trapezoidal. Posterior margins of fixigenae in *Zbirovia* are slightly downwardly curved in contrast to *Zdicella*, in which they are straight. *Zdicella* also possesses long genal spines and a semicircular pygidium. *Ulugtella,* which is probably also blind, has nine thoracic segments, semi-elliptical pygidium, longer pygidial axis and narrower doublure.

Zbirovia Šnajdr, 1956 resembles *Stenopareia* but *Stenopareia* differs in having eyes, and an oval pygidium, while *Zbirovia* has more steeply inclined lateral borders to the pygidium.

It is clearly different from other illaenids in having no eyes, outwardly curved and short axial furrows, semicircular outline of the cephalon, ten thoracic segments and trapezoidal outline to the pygidium with a large doublure.

Probably only one species, *Zbirovia arata* (Barrande, 1872), occurs in the Llanvirn to Ashgill of the Czech Republic (Šnajdr 1956, 1957).

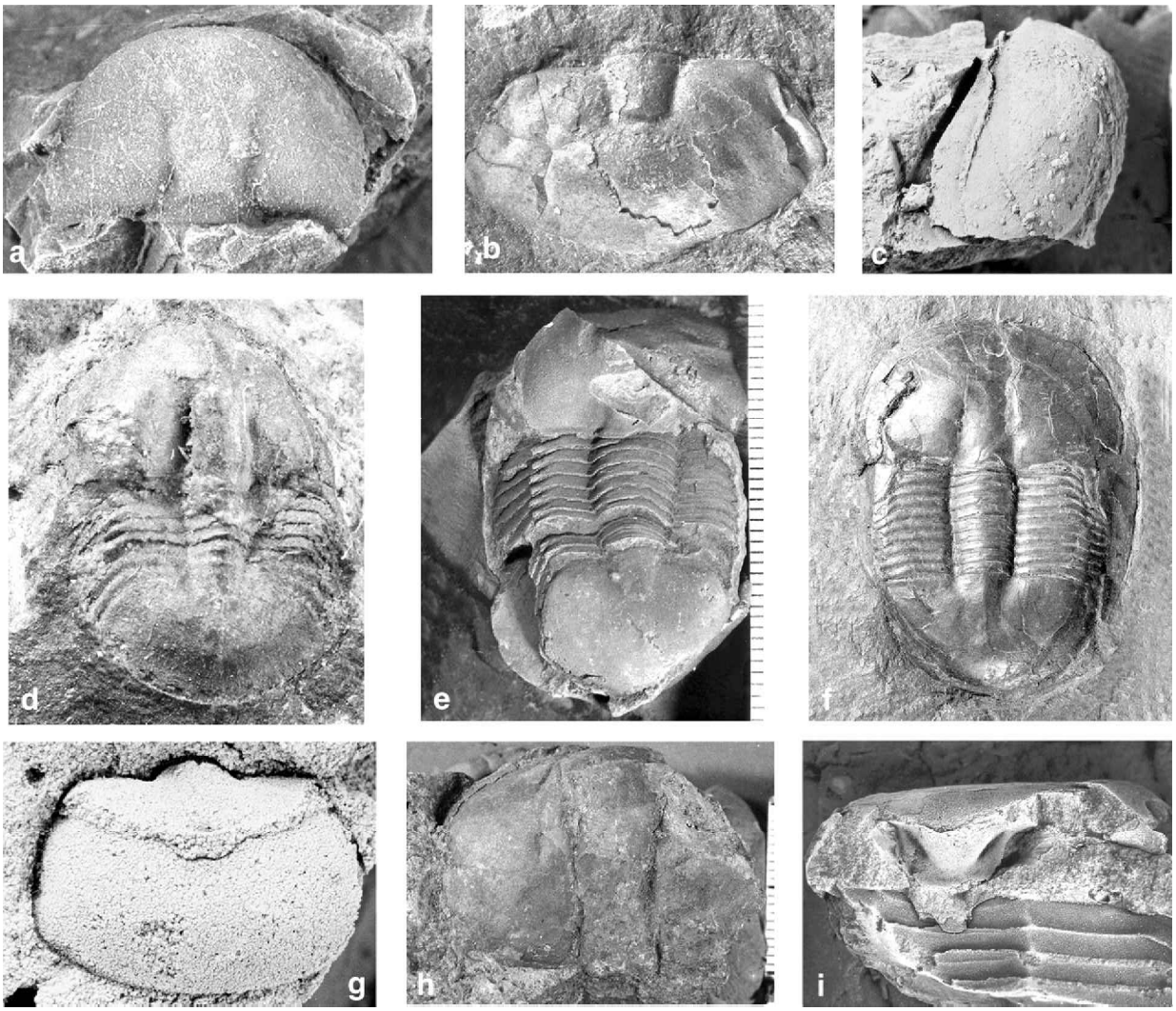

Figure 15 *Zbirovia arata* (Barrande, 1872): (a) cranidium NM L 33039, ×5, Vinice Formation, Chrustenice; (b) unwhitened pygidium NM L 16955, lectotype, ×3·5, Dobrotivá Formation, Sv. Dobrotivá; (c) cephalon in lateral view NM L 36013, ×2·4, Vinice Formation, Chrustenice; (e) almost complete specimen CGU JV 1480, ×1·5, Dobrotivá Formation, Praha-Vokovice; (g) pygidium NM L 19268, ×3·3, Libeň Formation, Rumpál. *Alceste latissima* Hawle et Corda, 1847; (d) meraspid specimen with three unreleased segments of transitory pygidia, holotype, NM L 15712, ×8, Králův Dvůr, Králův Dvůr Formation; (h) unwhitened cranidium NM L 20414, ×1·3, Králův Dvůr Formation, Kosov. *Zdicella zeidleri* (Barrande, 1872); (f) complete unwhitened specimen, lectotype, NM L 16660, ×1·3, Králův Dvůr Formation, Lejškov; (i) hypostome *in situ* CGU MŠ 750, ×1·1, Králův Dvůr Formation, Chodouň.

Zbirovia arata (Barrande, 1872)
(Fig. 15a–c, e, g)

1872 *Illaenus aratus* Barrande; Barrande, p. 68, pl. 14, figs 43, 44.
1913 *Illaenus perneri* Klouček; Klouček, pp. 3–6, pl. 1, figs 1, 2.
1913 *Illaenus perneri* mut. Klouček; Klouček, pl. 1, fig. 3.
1916 *Illaenus perneri*? var. *glabra* Klouček; Klouček, pp. 4, 14.
1918 *Illaenus aratus* Novák; Perner, pp. 20, 28, pl. 2, figs 27, 28.
1954 *Ectillaenus aratus* (Barrande); Jaanusson, p. 577.
1956 *Zbirovia arata* (Barrande); Šnajdr, pp. 490–92, pl. 1, figs 5–7.
1957 *Zbirovia arata* (Barrande); Šnajdr, pp. 189–93, pl. 4, figs 8–12.
1970 *Zbirovia arata* (Barrande); Horný & Bastl, pp. 60, 239, pl. 8, fig. 6.
1989 *Zbirovia arata* (Barrande); Pek & Vaněk, pp. 18, 47.
1992 *Zbirovia arata* (Barrande); Hammann, pp. 71, 72.
1997 *Zbirovia arata* (Barrande); Hammann & Leone, p. 92.

Lectotype. Pygidium NM L16955 from the Dobrotivá Formation at St. Dobrotivá. Figured by Barrande (1872, pl. 14, fig. 44). Lectotype designated by Šnajdr (1956).

Other material. Several complete specimens, tens of cephala and pygidia.

Diagnosis. *Zbirovia* species possessing semicircular cephalon with distinct outwardly curved axial furrows reaching half of the cephalic length in palpebral view. Eyes absent, facial suture moderately curved. Ten thoracic segments. Pygidium trapezoidal with strongly obliquely sloping lateral margins.

Description. Cephalon semicircular in outline, vaulted and longer than pygidium. In its anterior part it bends perpendicularly downwards. Anterior border of cephalon moderately arched, with a narrow margin. Arched axial furrows extending maximally to half of the cephalic length, in palpebral view. Glabella narrow and fixigenae wide. Several specimens show posterior border furrows and occipital ring. Glabella with pairs of oval anterior and middle, circular occipital and basal kidney-shaped muscle scars.

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Facial sutures arched in lateral direction, librigenae wide, eyes absent. Doublure of librigenae covered by dense terrace lines.

Rostral plate trapezoidal in outline, wide with 5–6 terrace lines.

Thorax consisting of ten segments.

Pygidium trapezoidal in outline with gently curving and steeply declined posterior margin. Lateral margins of pygidium in the first third of its width obliquely sloping. Axis weakly developed, short. Pygidial doublure wide, reaching two-thirds of the pygidial length (sag.) in dorsal view.

Surface sculpture of dense, fine pitting, which is reduced where the muscle scars are present and in the anterior part of the cephalon.

Ontogeny. Cephalon (NM L 32981) of probable meraspid or early holaspid specimen resembling the cephala of older holaspids. In the middle part of cephalon a keel-like elevation is developed and in the posterior part an occipital ring and posterior border furrows are present. Axial furrows longer than in the older holaspid specimens.

Remarks. Klouček (1913) defined his new species *Illaenus Perneri* and in 1916 the subspecies *Illaenus Perneri*? var. *glabra* from the Nučice Iron Ore Horizon of the Vinice Formation (Caradoc). Šnajdr (1956, 1957) correctly recognised that they belong in *Z. arata*.

Z. arata differs from other illaenids in having a semicircular cephalon with no eyes, short and distinct outwardly curved axial furrows, ten thoracic segments, trapezoidal pygidium with indistinct axis and very wide doublure.

Occurrence. From the Dobrotivá to the Vinice formations, Czech Republic.

Genus *Zdicella* Šnajdr, 1957

Type species. *Illaenus zeidleri* Barrande, 1872 from the Králův Dvůr Formation at Lejškov, Czech Republic.

Diagnosis. Genus with cephalon and pygidium semicircular, glabella narrow with straight short furrows occupying half of the cephalic length in palpebral view. Very long genal spines reaching the first third of pygidial length in dorsal view. Thoracic axis tapering gently backwards, pygidium semicircular.

Remarks. *Zdicella* was originally defined by Šnajdr, 1957. Whittington (1963) noted the resemblance between *Harpillaenus* (Whittington, 1963) and *Zdicella* but judged that this may be an example of homeomorphy rather than an indication of relationships. Gutiérrez-Marco & Rábano (1987) and Hammann & Leone (1997) considered *Zdicella* to be a synonym of *Delgadoa* Thadeu, 1947, while Dean *et al.* (1999) believed *Zdicella* and *Ulugtella* to be separate genera. As suggested by Hammann & Leone (1997), *Zdicella* is very similar to *Delgadoa* but the presence of radiating ribs on the pygidium of *Delgadoa* cannot be considered as the indicator of only a separate species. *D. loredensis* (Delgado, 1897) which is very similar to *Zdicella zeidleri* differs in having a more sharply tapering thoracic axis posteriorly, longer pygidium (sag.) and in the presence of radiating ribs.

It differs from *Ulugtella* and other illaenids in having long genal spines, a very narrow glabella and ten thoracic segments. *Ulugtella bornholmiensis* (Kielan, 1960), previously attributed to *Zdicella*, possesses shorter genal spines. *Z. zeidleri* is distinguished from other illaenids of the Bohemian Ashgill by its long genal spines, ten thoracic segments and flat morphology.

Zdicella occurs only in the Ashgill of the Czech Republic (Šnajdr 1957) and is represented by *Z. zeidleri* (Barrande, 1872). Kielan (1960) attributed *Z. bornholmiensis* Kielan, 1960 to *Zdicella*, but it was reassigned to *Ulugtella* by Hamman & Leone (1997); this approach is followed here.

Zdicella zeidleri (Barrande, 1872)
(Fig. 15f, i)

1872 *Illaenus zeidleri* Barrande; Barrande, p. 74, pl. 3, figs 23–29.
1918 *Illaenus zeidleri* Barrande; Perner, pl. 2, figs 15, 16.
non 1952 *Zdicella sola* (Barrande); Marek, p. 437, pl. 2, fig. 4. (= *Zdicella zeidleri*)
1954 *Ectillaenus zeidleri* (Barrande); Jaanusson, p. 577.
1957 *Zdicella zeidleri* (Barrande); Šnajdr, pp. 225–32, pl. 5, figs 1–6.
1970 *Zdicella zeidleri* (Barrande); Horný & Bastl, p. 329.
1983a *Zdicella zeidleri* (Barrande); Šnajdr, p. 11, pl. 2, fig. 2.
1989 *Zdicella zeidleri* (Barrande); Pek & Vaněk, p. 31.
2000 *Zdicella zeidleri* (Barrande); Shaw, pp. 377–8, pl. 1, figs 22, 23.
2000 *Zdicella sola* (Barrande); Shaw, p. 378, pl. 1, fig. 6.

Lectotype. Complete specimen NM L 16660 from the Králův Dvůr Formation at Lejškov. Figured by Barrande (1872, pl. 3, figs 20–22). Lectotype designated by Šnajdr (1957).

Other material. Twenty complete specimens, several tens of cephala and pygidia.

Diagnosis. See the diagnosis of *Zdicella*.

Description. Cephalon semicircular in outline, moderately vaulted. Glabella narrow. Axial furrows slightly curving outwards, occupying maximally half of the cephalic length in palpebral view. Lateral glabellar muscle scars crescentic, occipital scars circular, basal scars kidney-shaped, middle and anterior muscle scars oval.

Facial suture arched laterally, eyes absent. Librigenae extend to the exceptionally long genal spines, which terminate at the anterior third of the pygidium, tapering off at first rapidly, then more gently.

Rostral plate trapezoidal in outline, narrow with semicircular anterior margin. Middle hypostomal lobe minute and vaulted. Doublure of librigenae narrower than librigenae. Rostral plate and hypostome bearing terrace lines parallel with the anterior margin of rostral plate and the lateral margins of the cephalon.

Thorax composed of ten segments tapering gently backwards.

Pygidium slighty smaller than cephalon (and so would leave a gap on enrolment) and semicircular in outline with straight and wide anterior margin. Weakly distinct pygidial axis reaches maximally half of the pygidial length in dorsal view. Doublure narrow with terrace lines.

Exoskeleton bears dense pitting.

Ontogeny. In 1876 O. Novák lectured on the ontogeny of trilobites (notice in the journal *Vesmír*, 1876) and described an almost complete ontogenetic series of ten stages of *Zdicella zeidleri*. Unfortunately this material was probably lost. Younger holaspid or meraspid specimens bear shorter genal spines and longer axial furrows.

Occurrence. Králův Dvůr Formation, Czech Republic.

Genus *Alceste* Hawle et Corda, 1847

Type species. *Alceste latissima* Hawle et Corda, 1847 from the Králův Dvůr Formation at Králův Dvůr, Czech Republic.

Remarks. *Alceste* was originally defined by Hawle & Corda 1847, based on a meraspid specimen of *A. latissima* Hawle et

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Corda, 1847. Barrande (1852) considered the type species as *Illaenus hisingeri*. For more than 140 years *A. latissima* was regarded as a dubious species until Šnajdr (1983a) compared the holotype with late meraspid specimens of other illaenids from the Králův Dvůr Formation (Ashgill) and demonstrated that *A. latissima* is indeed a separate and valid species.

Recently Shaw (2000) discussed the validity of this genus and species. He suggested that this species name and its dependent genus should be retained, as based on the type specimens. The holaspid specimen described by Šnajdr (1983a) he considered to be a representative of *Zdicella*. He also suggested that *A. latissima* may well be the senior synonym of *Octillaenus hisingeri*.

The cranidium described by Šnajdr (1983a, b) might actually represent *Zdicella zeidleri* but it differs in having very long, deep glabellar furrows reaching the anterior border of cranidium. *Z. zeidleri* in contrast possesses shorter furrows reaching half of the cephalic length (sag.). The meraspid specimen is also distinguished from other Ashgill illaenid meraspids by its long, deep glabellar furrows and narrow glabella. In considering the synonymy of *O. hisingeri*, I follow the opinion of Šnajdr (1983a, b).

The validity of this species is still doubtful, and will remain so until more favourably preserved specimens are discovered.

It differs from other illaenid trilobites in having long, well-developed axial cephalic furrows and consequently a narrow glabella. It is distinguished from *Ulugtella* in having longer axial cephalic furrows reaching the anterior border of the cephalon, and a narrower glabella.

Alceste is known from the Caradoc to Ashgill of the Czech Republic (Šnajdr 1983b), Spain (Hammann 1992) and China (Tripp *et al.* 1989). In the Czech Republic it is represented by *A. latissima* Hawle et Corda, 1847.

Alceste latissima Hawle et Corda, 1847
(Fig. 15d, h)

1847 *Alceste latissima* nob.; Hawle & Corda, p. 66, pl. 4, fig. 31.
1852 *Illaenus hisingeri* Barrande; Barrande, p. 681, pl. 29, figs 25–29.
1957 *Octillaenus hisingeri* (Barrande); Šnajdr, pp. 154, 155.
1970 ?*Octillaenus hisingeri* (Barrande); Horný & Bastl, p. 189.
1983a *Alceste latissima* Hawle et Corda; Šnajdr, pp. 9–11, pl. 1, figs 1, 2.
1983b *Alceste latissima* Hawle et Corda; Šnajdr, p. 167, pl. 7, fig. 2.
1989 *Alceste latissima* Hawle et Corda; Pek & Vaněk, p. 17.
2000 *Alceste latissima* Hawle et Corda; Shaw, p. 375, pl. 1, fig. 2.

Holotype. A complete meraspid specimen NM L15172 from the Králův Dvůr Formation at Králův Dvůr. Figured by Hawle & Corda (1847, pl. 4, fig. 31).

Other material. An incomplete cranidium of a holaspid trilobite.

Diagnosis. *Alceste* species with cranidium oval in outline, wide (tr.). Fixigenae wide (tr.) and vaulted. Pygidium with narrow (tr.) pygidial axis.

Description. The only known holaspid cranidium is deformed and poorly preserved. It is large (sag. length 27 mm), strongly vaulted and probably originally oval in outline. Glabella narrow, vaulted. Long, well-incised and moderately curving axial furrows extending to the anterior margin of the cephalon. Facial sutures outwardly arched. Fixigenae wide (tr.) and vaulted, probably no eyes. Rostral plate and hypostome unknown.

Thorax and pygidium of holaspid specimens unknown.

Ontogeny. The holotype of this species is an almost complete, strongly deformed meraspid specimen with four released thoracic segments. Cephalon semicircular in outline. Glabella narrow with long axial furrows. Pygidium oval in outline with well-defined, narrow and long axis.

Remarks. As noted in the remarks on the genus, for more than 140 years this species was included in the synonymy of *O. hisingeri* until Šnajdr (1983a, b) emended the diagnosis with a description of a holaspid cranidium. It differs from *O. hisingeri* in its long, narrow glabella and also in the absence of eyes.

A. rugosa Hammann, 1992 from the Ashgill of Spain has a cranidium semicircular in outline, while in *A. latissima* it is oval. *A. latissima* also possesses wider (tr.) fixigenae. *A. longifrons* (Olin, 1906), previously ascribed to *Zbirovia* by Kielan (1960), is very similar to the species discussed here and it is not impossible that it represents the younger synonym of *A. latissima*, as suggested by Hammann (1992).

Occurrence. Králův Dvůr Formation, Czech Republic.

Genus *Svobodapeltis* Šnajdr, 1957

Type species. *Bumastus avus* Holub, 1908 from the Šárka Formation at Osek near Rokycany, Czech Republic.

Diagnosis. Parabolic outline of cephalon, very wide (tr.) glabella and thoracic axis. Fixigenae narrow (tr.). Segments of thorax short (tr.), pygidium parabolic with indistinct axis and narrow doublure.

Remarks. *Svobodapeltis* resembles *Bumastus* Murchison, 1839 but it differs in having larger fixigenae, smaller eyes and a facial suture, which is shorter and strongly curved. *Svobodapeltis* is represented by only one species *S. avus* (Holub, 1908), restricted to the Šárka Formation of the Czech Republic.

Svobodapeltis avus (Holub, 1908)
(Fig. 16a–b)

1908 *Bumastus avus* Holub; Holub, p. 12, pl. 1, fig. 2.
1916 *Bumastus avus* Holub; Klouček, p. 10.
1916 *Bumastus pragensis* Klouček n. sp.; pp. 10, 11.
1957 *Svobodapeltis avus* (Holub); Šnajdr, pp. 243–6, pl. 12, figs 1, 2.
1970 *Svobodapeltis avus* (Holub); Horný & Bastl, pp. 64, 66, 246.
1989 *Illaenus pragensis* (Klouček); Pek & Vaněk, p. 17.

Lectotype. Pygidium MR 1–1202 from the Šárka Formation at Osek near Rokycany. Figured by Klouček (1916, pl. 1, fig. 2).

Other material. Seven pygidia and one incomplete damaged specimen.

Diagnosis. See the diagnosis of *Svobodapeltis*.

Description. Cephalon vaulted, semicircular in outline with a moderately parabolic anterior part. Glabella wide, axial furrows strongly curving outwards in the first third of the cephalon and extending over half of the cephalic length in palpebral view. Lateral pairs of muscle scars crescentic, occipital, basal, middle and anterior pairs oval.

Fixigenae narrow, slightly narrower in their anterior part. Librigenae narrow, triangular in outline with rounded posterior edge. Eyes large, located in the posterior part of the cephalon, with elevated palpebral lobes.

Rostral plate and hypostome unknown.

Thorax composed of ten segments. Axis is wider (tr.) than pleurae.

Pygidium moderately parabolic in outline, vaulted, with poorly defined and short pygidial axis. Doublure narrow.

Surface sculpture of dense and fine pitting.

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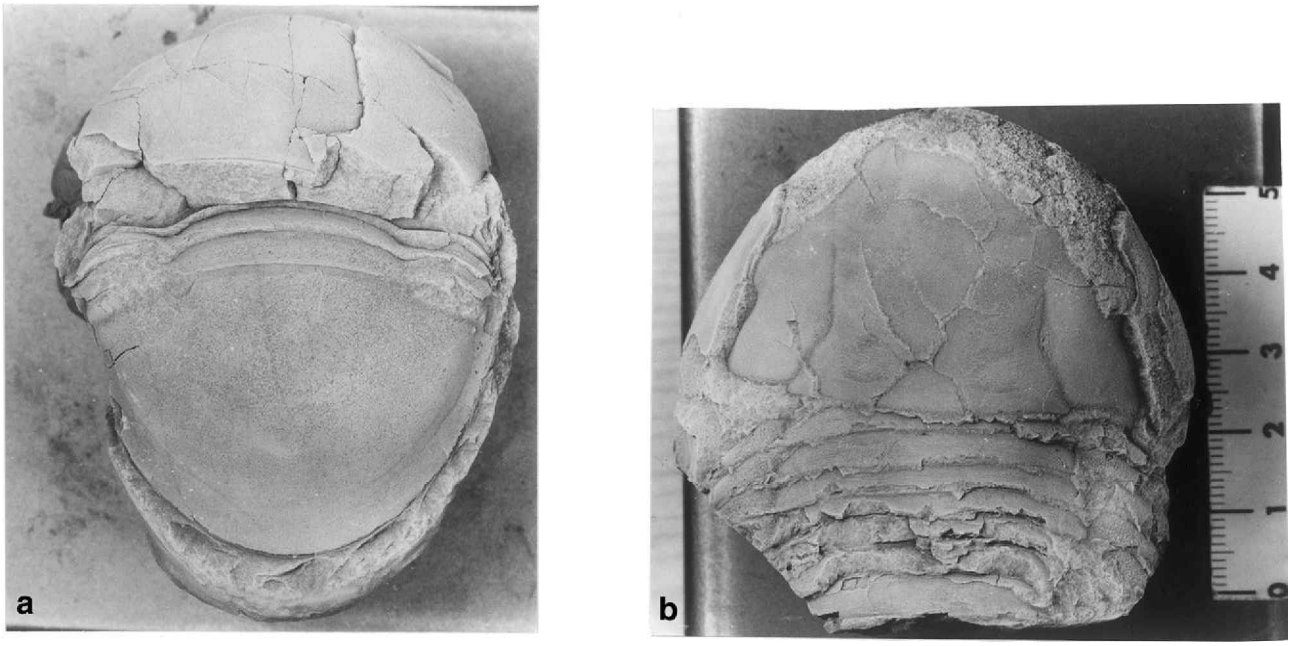

Figure 16 *Svobodapeltis avus* (Holub, 1908): (a) incomplete specimen NM L 19296, ×1·2, Šárka Formation, Praha-Vokovice; (b) cephalon with incomplete thorax NM L 19281, ×2, Šárka Formation, Praha-Šárka.

Remarks. *Bumastus pragensis* Klouček (1916) from the Šárka Formation is a synonym of *S. avus*. Pek & Vaněk (1989) assigned *S. avus* to *Illaenus* Dalman, 1827. In contrast to the type species of *Illaenus*, *S. avus* possesses a circular cephalon with smaller eyes, which do not have elevated palpebral lobes, wider (tr.) glabella and thoracic axis, narrower (tr.) fixigenae and parabolic outline of the pygidium with indistinct axis. These morphological details also distinguish *S. avus* from other illaenids.

Occurrence: Šárka Formation, Czech Republic.

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